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A PRELIMINARY REVISION OF TRAGIA (EUPHORBIACEAE) IN THE UNITED STATES[1]

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The genus *Tragia* (Crotonoideae — Acalypheae) comprises about 150 species of nettle-like plants which are widely distributed in tropical and subtropical or warm-temperate regions of both the New World and Old World. It is by far the largest and most diverse of the 19 genera of subtribe Plukenetiinae recognized by Pax and Hoffman (1919), and various generic segregates have been proposed during the past 150 years.

In the New World, the center of diversity of *Tragia* is in Brazil, and only about 20 species have been recorded from North America. These include some taxa of particular phylogenetic interest, however, for *T. bailloniana* from Mexico and Central America may be one of the most primitive species in the genus. The present study has been deliberately restricted in scope to include only those taxa represented in the United States, because it seems to us that the collections available from Mexico are at present inadequate to serve as the basis of even a preliminary treat-

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1. This study incorporates part of a doctoral dissertation submitted by the senior author in partial fulfillment of the requirements for the Doctor of Philosophy degree at Purdue University. Investigations were supported by grants from the Purdue Research Foundation and (for the junior author) the National Science Foundation and the John Simon Guggenheim Memorial Foundation while at the Gray Herbarium, Harvard University. The assistance of Dr. Lillian Miller and Miss Jeanie Taylor is gratefully acknowledged.

ment (at least in the absence of field work in critical areas of the Mexican plateau). Mexican specimens of the *T. nepetifolia* complex have been examined in order to relate them to those from the United States, and it is hoped that a revision of the Mexican species can eventually be added to the present work in order to account for all of the North American taxa.

NOMENCLATURAL HISTORY

The genus *Tragia* was originally established by Plumier (1703) on the basis of the American species designated by Linnaeus as *T. volubilis*. The first comprehensive revision of the group was that of Baillon (1858), who recognized no less than 10 genera within the concept of *Tragia* held by A. Jussieu (1824). Doubtless Baillon's disposition was extreme, but some of the taxa such as *Leptorachis*, *Ctenomeria*, *Bia*, and *Zuckertia* are very distinctive and have been regarded as worthy of generic status by a few workers.

The first detailed enumeration of all the taxa of *Tragia* in anything approaching a modern sense was that of Mueller Argoviensis (1865, 1866), who accepted *Leptorachis* as a distinct genus and recognized 11 sections to accommodate the 49 species then known for *Tragia*. In the 'Flora Brasiliensis' (1874), Mueller reduced *Leptorachis* to a section of *Tragia*, a disposition which was followed by Bentham (1880) and Pax (1890).

In the last general revision of *Tragia*, Pax and Hoffmann (1919) reduced the number of sections to 9 while accepting 123 species, 58 of these American and 65 Old World; only one species, *T. volubilis*, was recorded for both the Eastern and Western Hemispheres, and it is presumed to be American in origin. Pax and Hoffmann rather slavishly followed Mueller in placing the U. S. taxa of *Tragia* into two sections: *Leucandra* and *Eutragia*; they thus perpetuated Mueller's error in putting specimens of *T. ramosa* in two different sections under two species names (*T. ramosa* and *T. nepetifolia*). However, by recognizing *T. teucriifolia* [*T. brevispica*] and *T. amblyodonta* as distinct, they raised the number of species occurring in the United States to 11.

Johnston (1962) has reviewed some of the systematic problems presented by the taxa in the Southwest, which he refers to as 'noseburns' (from the effects of the stinging foliage on grazing stock). He has correctly pointed out that the distinction between sections *Leucandra* and *Tragia,* at least as construed by Pax and Hoffmann, is very weak. It seems clear that this supposed sectional distinction, at least as applied to taxa in the United States, cannot be maintained.

On the basis of his inability to find stable, geographically correlated morphological characters in the Southwestern noseburns, Johnston has placed all of the plants in the complex under a single species name, *T. nepetifolia* Cav., and relegated no less than 18 names to synonymy. It is indeed evident that the noseburns are bewilderingly variable in habit and leaf shape as well as in number of flower parts. The plasticity of individual plants in responding to environmental variations and the large amount of intra- and interpopulation diversity, together with the often fragmentary nature of available herbarium specimens, results in a baffling pattern of variation which frankly cannot always be untangled even after the most intensive study.

Nevertheless, a detailed analysis of specimens from throughout the southern United States, combined with field studies in the Gulf States and Texas (Miller 1964), has shown that there are morphologically recognizable taxa among the noseburns which do have distinctive geographical ranges. Consequently, we are unable to concur with Johnston's conclusion that the Southwestern noseburns all belong to a single species. Amalgamation of all these populations into one species appears to be contradicted by the geographical correlations noted above as well as by *(inter alia)* the following facts: (1) the chromosome complement in at least one taxon, *T. amblyodonta,* appears to be decaploid ($n = 55$), whereas the other noseburns investigated cytologically are tetraploids ($n = 22$); (2) peculiar horned fruits similar to those of the widespread tropical vine *T. volubilis* occur only on plants with the leaf shape and flow-

ers of *T. brevispica*; (3) the female calyx-lobes of plants assigned to *T. betonicifolia* are on the average much longer than those of related species; (4) typical specimens of *T. ramosa* have styles which are slender and much smoother (scarcely or not papillate) than those of related taxa, including *T. nepetifolia*.

On the basis of all of the evidence, we have concluded that 5 species of noseburns should be distinguished where Johnston has recognized only one; this results in a total of 13 species for the United States instead of the 9 or 10 which would be recorded in accordance with his concept. It must be admitted that the system presented here is not an especially tidy one, as a considerable number (ca. 5-10%) of the specimens examined remain dubious or unassignable, and the disposition of some of the taxa (in particular *T. leptophylla*) is still doubtful. However, the degree of difficulty encountered in annotating the often fragmentary herbarium specimens or in identifying them by means of a key should not be confused with the problem of whether there are really any distinctions between the wild populations. Our conclusion that there are 5 U. S. species of noseburns in the *T. nepetifolia* complex is not founded on irrefutable proofs, but it is at least a reasonable hypothesis which is deserving of criticism and verification by systematists in the Southwest.

MORPHOLOGY

GROWTH FORM. All of the U. S. species of *Tragia* are perennial herbs with a woody taproot and alternate leaves. The stems may be either erect, decumbent, or twining; within a single species both twining and non-twining types may occur. At one end of the spectrum, such species as *T. nigricans* and *T. saxicola* have never been observed to twine, while on the other hand *T. glanduligera* and *T. cordata* are always twining. In *T. ramosa* and some related species there appears to be considerable amplitude of habit, as otherwise similar plants may be either erect, decumbent or twining. These differences, which may reflect ecotypic

variation in some instances and simple adaptability in others, need to be more carefully studied.

LEAVES. The leaves of *Tragia* are quite variable in both size and shape, but within a broad range are sufficiently distinctive to present useful taxonomic characters. The petioles, which vary in length from less than 1 mm in *T. urens* to over 8 cm in *T. cordata*, have 5 free vascular traces. The leaf-blades vary from linear and entire in some forms of *T. urens* to serrate or dentate in most species, while in the rare *T. laciniata* the blades are tripartite with coarsely toothed lobes. Stomata occur on both upper and lower surfaces, but are more numerous below (they may be restricted to areas along the major veins on the upper surface). Most of the stomata are of the 'rubiaceous' type as defined by Metcalfe and Chalk (1950), but sometimes they may approach the 'cruciferous' type (Miller 1964). The stomata of *T. amblyodonta* are outstanding in being strikingly larger than those of related species: mean values are 26.6μ for the upper epidermis and 22.0μ for the lower, as opposed to 20.7μ and 18.3μ in *T. nigricans*, the species with the next largest stomata. It seems probable that this larger stomatal size of *T. amblyodonta* is correlated with its high degree of polyploidy.

The most striking feature of the leaves of *Tragia* is the presence of characteristic stinging hairs, which have been described by Rittershausen (1892) and Knoll (1905). These hairs consist of an elongated central cell, which according to Knoll is of subepidermal origin, surrounded by 3-5 'jacket-cells'. An extremely sharp-pointed crystal at the distal end of the central cell acts as the piercing agent when the end of the hair is touched. The stinging hairs are much alike in all U. S. species of *Tragia*, although there is a tremendous variation in the painfulness of the sting; *T. amblyodonta* appears to be the worst offender, whereas *T. urens*, despite its suggestive epithet, stings little or not at all. Possibly the most important variable is the quantity and nature of the proteinaceous poisoning element which is released when the end wall of the cell pulls back and per-

mits the sharp crystal tip to penetrate the skin. Stinging hairs are also found on the stems, inflorescence axes, calyces, and ovaries, and may be very prominent on the ripened fruit.

Unicellular hairs are also present on the stems and leaves, usually intermixed with the stinging ones. Long-stalked multicellular glandular hairs occur on the inflorescences of *T. glanduligera* intermixed with both other types; this condition is common in various tropical taxa but is not known in other U. S. species, although a few minute short-stalked glandular hairs may be found on the inflorescence.

INFLORESCENCE. In all of the U. S. taxa of *Tragia*, the inflorescence is an androgynous raceme (fig. 1) with one female flower (rarely two) at the base and 3-20 (or more) male flowers at the distal nodes. Our representatives have all flowers solitary in the axil of the subtending bract, but some tropical species may have several male flowers per bract. The staminate bracts are entire and more or less cucullate, while the female may be either entire or 3-lobed.

The position of the racemes of the U. S. species is consistently opposite the leaves, as pointed out by Johnston (1962), so that the racemes are actually terminal and the main stem axis is thus a sympodium. In some tropical species the situation is more complicated because the racemes terminate lateral branches (e.g., in *T. mexicana*), and the inflorescence pattern in temperate species is apparently derived by reduction. *Tragia urens* shows an approach to the condition in some of the tropical species in that the racemes are borne terminally on lateral leafy branches as well as at the upper nodes of the main stem; in this species, therefore, the lower part of the stem appears to be monopodial while the upper part is sympodial.

FLOWERS. The staminate pedicel is articulate, and the basal portion persists after the fall of the male calyx. The male pedicel is supplied with 2 vascular traces and the female with 5 (Miller 1964). The flowers are apetalous, the perianth being represented by a gamophyllous calyx; the union of the calyx-lobes may be slight, but it is always

Plate 1356.

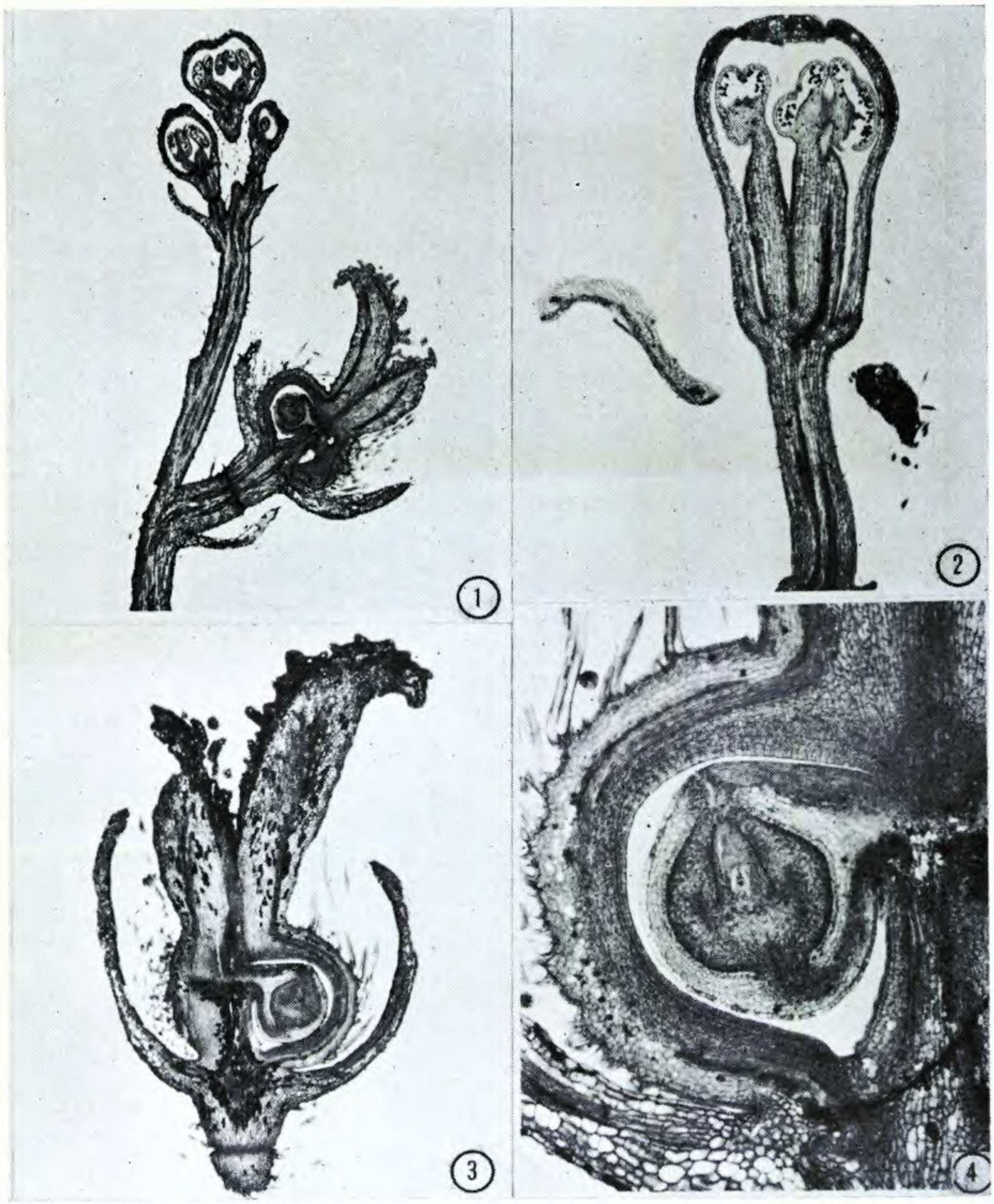


Fig. 1. Longitudinal section of inflorescence, *Tragia nigricans*, showing androgynous arrangement of flowers, × 20 (*K. & L. Miller 1173*).

Fig. 2. Longitudinal section of staminate flower, *Tragia nigricans*, showing connate filaments, × 60 (*K. & L. Miller 1173*).

Fig. 3. Longitudinal section of pistillate flower, *Tragia urticifolia*, showing papillate stigmatic surface, stigmatoid tissue in stylar column and single anatropous ovule, × 30 (*K. & L. Miller 848*).

Fig. 4. Longitudinal section of ovary, *Tragia urticifolia*, showing anatropous ovule and obturator, × 100 (*K. & L. Miller 848*).

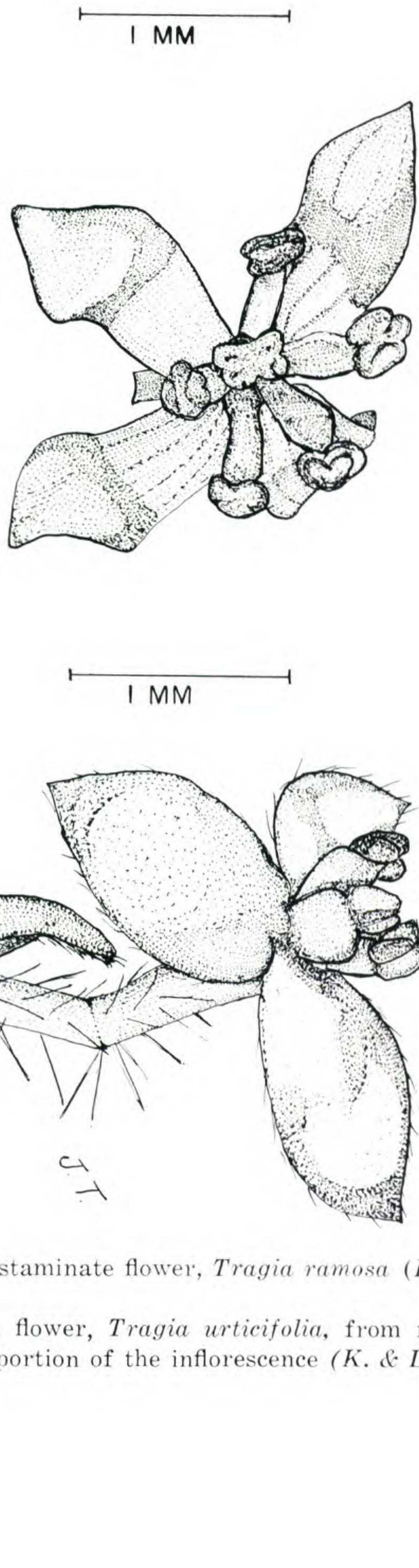


Fig. 5. Terminal staminate flower, *Tragia ramosa* (*K. & L. Miller 1341*).

Fig. 6. Staminate flower, *Tragia urticifolia*, from near the middle of the staminate portion of the inflorescence (*K. & L. Miller 848*).

evident, and the lobes never disarticulate separately from the receptacle. The staminate flowers (fig. 2) have mostly 3 or 4 valvate calyx-lobes per flower, but the number may fluctuate within a single inflorescence, depending on the species. The pistillate calyx nearly always consists of 2 whorls of 3 lobes each, which unlike the male are imbricate in the bud. Both male and female calyx-lobes usually possess 3 veins which are however more elaborately branched in the female.

ANDROECIUM. In the vast majority of plants of *Tragia* in the United States, the androecium consists of 3 to 5 stamens (fig. 6), the number varying over this range within a single inflorescence in many species. However, *T. smallii* and *T. urens* ordinarily have only 2 stamens (very rarely 3). The filaments, which may be thickened and fleshy or rather slender, are supplied with a single vascular trace; in most species, they are connate only at the base, but in *T. nigricans* they may be fused for half or more their length. There is usually a small pistillode in the center of the flower between the connate bases of the stamens.

The stamens and calyx-lobes of the terminal male flower are commonly more numerous than those of the axillary flowers of the inflorescence, there being usually 4 to 6 calyx-lobes and 5 to 8 stamens (fig. 5). Johnston (1962) described this terminal flower as "probably representing the monstrous joining of 2 or more flowers". However, such terminal flowers were found to occur more or less regularly in most of the U. S. species, although of course they might not be evident on partially-grown racemes. It is rather difficult, therefore, to see how the terminal flowers are any more "abnormal" than are e.g. the first-produced cyathia of *Euphorbia*, which may often have an increased number of floral parts (Croizat, 1942). It is possible, as Johnston suggests, that the larger number of parts of terminal male flowers may have added to the taxonomic confusion, since both Mueller (1866) and Pax and Hoffmann (1919) separated *T. ramosa* (as *T. stylaris*) into a separate section

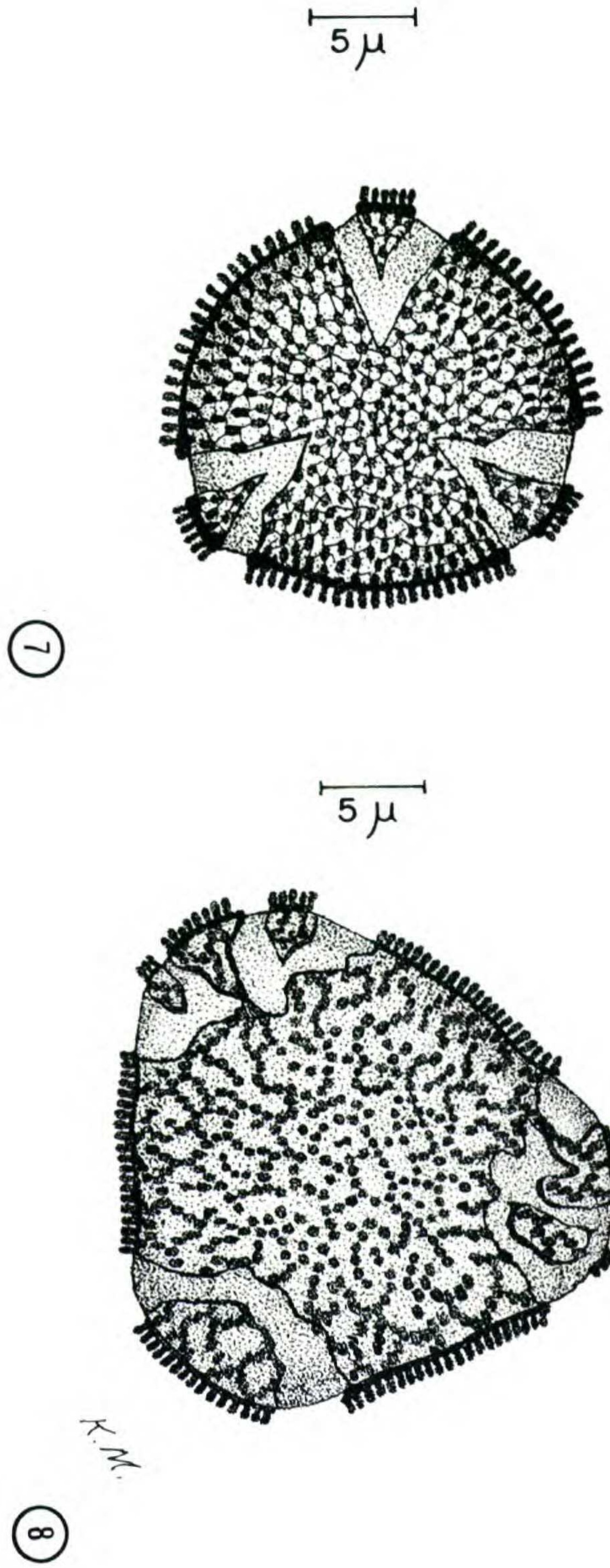


Fig. 7. Pollen grain, *Tragia ramosa* (*K. & L. Miller 1341*).

Fig. 8. Pollen grain, *Tragia smallii* (*K. & L. Miller 865*).

from *T. nepetifolia* on a supposed difference in stamen number.

POLLEN GRAINS. The most extensive previously published treatment of the microspores of *Tragia* is that of Punt (1962), who described the variation among 8 species, and also contributed some interesting speculations about taxonomic relationships in the subtribe Plukenetiinae. Punt distributed the 8 species of *Tragia* studied into 4 morphological groups: (1) inaperturate, intectate, pilate *(T. fallax, T. sellowiana):* the '*Tragia fallax* type'; (2) tricolpate, intectate, pilate *(T. geraniifolia, T. ramosa, T. tristis, T. volubilis):* the '*Tragia tristis* subtype' (groups 2, 3, and 4 all being placed in the '*Plukenetia* type'); (3) tricolporate, intectate, reticulate *(T. stolziana):* the '*Plukenetia verrucosa* subtype'; and (4) tricolpate, tectate, psilate *(T. capensis):* the '*Plukenetia volubilis* subtype'.

TABLE 1. POLLEN SIZE IN NORTH AMERICAN SPECIES OF *Tragia*[2]

Section TRAGIA	*Voucher*	*Diameter in polar view (μ)* range	mean
T. amblyodonta	Miller & Miller 1178	21.3-26.4	23.4
T. betonicifolia	Miller & Miller 1350	19.6-23.0	21.2
T. brevispica	Cory 54778	18.7-22.1	20.7
T. cordata	Demaree 15378	21.3-25.5	24.0
T. glanduligera	Lundell & Lundell 10665	18.7-25.2	20.1
T. laciniata	Peebles et al. 5641	17.0-20.4	19.0
T. nepetifolia	Tucker 2449	17.0-20.4	18.4
T. nigricans	Miller & Miller 1173	23.0-25.5	24.5
T. ramosa	Miller & Miller 1167	17.9-22.1	19.9
T. saxicola	Curtiss 2517	22.1-26.4	24.8
T. urticifolia	Miller & Miller 848	22.1-27.2	24.6
Section LEPTOBOTRYS			
T. smallii	Miller & Miller 865	25.5-28.1	26.9
T. urens	Miller & Miller 776	20.4-26.4	22.9

Miller (1964) investigated the pollen of the 13 taxa occurring in the United States, using the glycerine jelly method of Wodehouse (1935) rather than the acetolysis method of Punt (Table 1). This led to the discovery that

2. [Table 1] Parameter estimates are based on measurements of 30 grains per specimen.

the tricolpate grains of the U. S. taxa have operculate colpi, a feature not mentioned by Punt, whose acetolyzed preparations evidently did not show any traces of the operculum. Because of the distinctness of the pila at outermost focus, most of the U. S. species (fig. 7) would fall into Punt's *Tragia tristis* subtype. However, it is actually extremely difficult to decide if these grains are truly intectate, as the pila may be proximally fused.

Two U. S. species, *Tragia smallii* and *T. urens*, were found to differ from any of those described by Punt. In these two plants of the southeastern United States the pollen grains (fig. 8) are rounded-triangular in optical section and have very broad pore-like colpi with net-like incrustations apparently representing the operculum of other species. The pila are furthermore partially united into an extremely fine reticulum, so that in some respects the grains might fit into Punt's *Plukenetia volubilis* subtype.

Examination of other neotropical species of *Tragia* indicates that most of them clearly fall into one or another of the groups listed above. Particularly interesting is *T. bailloniana*, which alone among the American taxa observed is distinctly reticulate, with even-margined colpi. It would therefore go into the *Plukenetia verrucosa* subtype adjacent to such African species as *T. stolziana* and *T. pungens*.

Punt (1962) has suggested that sect. *Bia* might perhaps be best treated as a distinct genus because of the inaperturate grains. However, in view of the rather wide spectrum of morphological variation which has already come to light, it would appear that the pollen of this section is not much more aberrant than that of some sections with colpate grains. Furthermore, such a genus would be extremely difficult to distinguish on the basis of floral characters. Because of the imperfect correlation between pollen characters and taxonomic boundaries, it still seems best to retain all of the sections of *Tragia* within a single genus.

GYNOECIUM. The gynoecium in *Tragia* is of a type rather widespread in the subfamily Crotonoideae, with 3 united carpels and a single anatropous ovule in each locule (fig. 3).

The styles are elongated, often with a conspicuously papillate stigmatic surface, and may be united up to half or more their length. The conducting tissue in the stylar canal is prolonged into each locule as a cap-like obturator appressed to the micropylar end of the ovule. An extension of the obturator, which is made up of closely packed filamentous cells, projects into the micropyle and is in contact with the nucellus. As in most genera of Euphorbiaceae, the obturator of *Tragia* is transient and atrophies during development of the seed.

The solitary pendent anatropous ovule (fig. 4) is typical of that found in many genera of the Crotonoideae, tribe Acalypheae: it is crassinucellate, with two thick integuments, both of which contribute to the formation of the micropyle. A peculiarity which the *Tragia* ovule shares with that of many Acalypheae is the very massive inner integument and the expanded chalazal region which is supplied with distinct vascular traces. The nucellus in Euphorbiaceous ovules of this kind lacks a beak, and as if in compensation the obturator often provides a direct contact between the tip of the nucellus and the transmitting tissue in the style.

FRUIT. The fertilized gynoecium of *Tragia* develops into a dry thin-walled capsule which dehisces more or less explosively at maturity. At dehiscence the cocci first separate septicidally and from the columella; the lateral walls split open along the line where the carpel and columella were attached; and the cocci also split on the abaxial side (loculicidally), allowing the seed to be thrown from the separated coccus. The vasculated exocarp of the coccus is in most species formidably armed with a dense array of stinging hairs; the non-vasculated endocarp is composed of radially elongated sclerified cells.

SEEDS. At the time of formation of the proembryo, the nucellus has been reduced to a plug adjacent to the micropyle, and the inner integument and chalaza are still massive. However, as the embryo develops the inner integument becomes partially replaced by endosperm; in the

mature seed its outer epidermis has become the hard palisade layer. The collapsed layers of the outer integument become flattened on the seed surface. The mature seeds are nearly spherical, with a smooth or slightly roughened more or less mottled coat.

CYTOLOGY. Miller (1963) first published counts of chromosome numbers in the genus *Tragia* for 5 U. S. species. With the addition of one species and correction of identifications, verified counts for 6 species are presented here (Table 2). It is obvious that the results presented here are barely a start, since only one population has been counted for each species, and 7 of the 13 U. S. species are still entirely unstudied. However, the chromosome studies do warrant the following observations.

TABLE 2. CHROMOSOME NUMBERS IN *Tragia* (Miller, 1963)[3]

	Voucher	*2n*
Section TRAGIA		
T. amblyodonta	Miller & Miller 1178	ca. 110
T. brevispica	Miller & Miller 1076	44
T. ramosa	Miller & Miller 1167	44
T. urticifolia	Miller & Miller 848	44
Section LEPTOBOTRYS		
T. smallii	Miller & Miller 882	44
T. urens	Miller & Miller 776	44

The six counts reported clearly establish that the base number in *Tragia* sect. *Tragia* and sect. *Leptobotrys* is $x = 11$. No counts are yet reported from species belonging to the other seven sections, and such information is particularly to be desired since the results might help to evaluate the status of taxa such as sect. *Bia*. Since no chromosome counts have been reported for any of the other 18 genera of Plukenetiinae recognized by Pax and Hoffmann, knowledge of the base number is not of any assistance in determining intergeneric relationships.

The finding of $n = 55$ in *T. amblyodonta* is interesting, since the other five U. S. taxa counted all agree in having

3. [Table 2] Two of the chromosome numbers reported in Miller (1963) were based on misdetermined specimens. The count reported for *T. glanduligera* was actually made on material of *T. brevispica*, and that reported for *T. ramosa* represented *T. amblyodonta*.

$n = 22$. This provides some support for our decision to recognize *T. amblyodonta* as a distinct species, rather than sinking it in *T. nepetifolia* as was done by Johnston (1962). The greater stinging capacity of *T. amblyodonta* would appear to be correlated with this in some way (larger cell size?).

RELATIONSHIPS

In the treatment of Pax and Hoffmann (1919), all of the U. S. species of *Tragia* were placed in sect. *'Eutragia'* except for *T. ramosa* and *T. brevispica*, which went into sect. *Leucandra*. As Johnston (1962) has pointed out, this disposition of *T. ramosa* and *T. brevispica* was based on an untenable supposed distinction in stamen number; since stamen numbers of 3-6 occur in all the noseburns, they cannot be separated into two sections by means of this character. Probably sect. *Leucandra*, if it is a valid taxon at all, will have to be characterized on some other basis; and in any event it is not represented by any species in the United States.

On the other hand, two U. S. species, *T. urens* and *T. smallii*, do seem to be rather sharply set off from their congeners by male flowers with only 2 stamens that produce a different sort of pollen. Although Mueller (1866) recognized a sect. *Leptobotrys* for *T. urens*, Pax and Hoffman (1919) merged it with their sect. *Eutragia*. We believe that this group originally recognized by Baillon and Mueller should be resuscitated in order to emphasize the considerable morphological gap between *T. urens*, *T. smallii* and the Southwestern noseburns.

The remaining 11 U. S. species must all be referred to sect. *Tragia*, but they do not seem to represent a cohesive phyletic unit, as at least 2 species may have their closest relationships outside our area (in Mexico). The nearest species to *T. cordata* may be *T. affinis* of western and central Mexico; the latter is strikingly similar in habit and leaf-shape, even though its male flowers (with 13-18 stamens) are very different. *Tragia glanduligera* is a primarily Mexican species which only enters extreme southern

Texas, and its immediate relationships must be with some taxon to the south.

The core of 9 species left after peeling off the elements mentioned does present the picture of a probably monophyletic — though certainly not a homogeneous — group. It may be analyzed into 1 cluster and 3 isolated species: (1) the noseburns proper, comprising *T. amblyodonta*, *T. betonicifolia*, *T. brevispica*, *T. nepetifolia*, *T. ramosa*, and *T. saxicola;* (2) *T. nigricans;* (3) *T. laciniata;* and (4) *T. urticifolia.* Relationships in the noseburn complex remain to be exactly elucidated, partly because of its tremendous unexplained variability. Hybridization between the noseburns — all of which are at least partly sympatric except for *T. saxicola* — may possibly account for some of the difficulty, although we have found it impossible to distinguish morphological aberrancy due to interspecific crossing from the protean plasticity of unhybridized populations. Cultivation under controlled conditions and experimental crosses will be necessary to have even a chance of resolving this problem. It does appear that ecological preferences may act to separate the taxa to some extent: for example, in Texas *T. betonicifolia* and *T. urticifolia* tend to occur on sandy or granitic soils, whereas *T. amblyodonta* and *T. brevispica* are usually found on limestone.

A further complication in assessing relationships among the noseburns is that several species also extend into Mexico. At least *T. amblyodonta*, *T. brevispica*, and *T. ramosa* are known to go south of the Rio Grande; and the population of *T. nepetifolia* in Arizona represents only a small northernmost extension of a primarily Mexican population. Although we have examined a considerable number of Mexican specimens, we have not attempted to account for the Mexican representatives of the noseburn complex in this paper, beyond establishing the typical element associated with the name *T. nepetifolia.* It is possible that thorough study of the Mexican taxa may reveal the name *T. nepetifolia* to be camouflaging as many different species as has proved to be the case in Texas.

Pax and Hoffmann (1919) remarked on the parallelism evident between the temperate or subtropical representatives of sect. *Tragia* in North and South America, pointing out 4 pairs of vicarious species: *T. pinnata* — *T. laciniata*, *T. bahiensis* — *T. glanduligera*, *T. geraniifolia* — *T. nepetifolia*, and *T. tenella* — *T. amblyodonta* (southern taxon listed first in each pair). There is also a certain resemblance between *T. paxii* of Argentina (Lourteig & O'Donell, 1941) and *T. brevispica* of Texas, particularly with regard to the crested fruits. It would appear that all these cases are indeed parallelisms, in the sense that the taxa involved are in each instance more closely related to species in their own area than to the antipodal vicariant; on the other hand, the overall resemblance between the taxa of Texas — northern Mexico with those of Argentina probably does reflect a genetic continuity in the past analogous with the bipolar distribution of *Prosopis* (Johnston, 1940) and a number of other subtropical taxa of the New World.

SYSTEMATIC TREATMENT

Approximately 2,500 specimens of *Tragia* were examined during this study. We wish to express our appreciation for the courtesies extended by the directors of the institutions listed below in allowing us to borrow or examine their material.

ARIZ University of Arizona, Tucson; BM British Museum (Natural History), London; FLAS University of Florida, Gainesville; G Conservatoire et Jardin Botaniques, Geneva; GA University of Georgia, Athens; GH Gray Herbarium, Harvard University, Cambridge; IA State University of Iowa, Iowa City; ISC Iowa State College, Ames; K Royal Botanic Gardens, Kew; KANU University of Kansas, Lawrence; KY University of Kentucky, Lexington; LL Texas Research Foundation, Renner; M Botanische Staatssammlung, Munich; MA Instituto Cavanilles, Madrid; MICH University of Michigan, Ann Arbor; MO Missouri Botanical Garden, St. Louis; NCSC North Carolina State University, Raleigh; NMC State University of New Mexico, University Park; NY New York Botanical Garden, New York; P Muséum National d'Histoire Naturelle, Paris; PH Academy of Natural Sciences, Philadelphia; PUL Purdue University, Lafayette; SMU Southern Methodist University, Dallas; TEX University of Texas,

Austin; UARK University of Arkansas, Fayetteville; UNM University of New Mexico, Albuquerque; USF University of South Florida, Tampa.

Future collectors of *Tragia* are hereby admonished to take careful notes on variation seen within natural populations, with particular reference to the following characters: (1) proportion of plants showing twining habit; (2) virulence of stinging hairs (this demands a certain amount of *noblesse oblige* on the part of the investigator); (3) color of male flowers; (4) presence of winged fruits (in populations from Texas).

A more complete list of specimen citations has been provided by Miller (1964), together with statistical analyses of some of the data. A tabulation of the historically important Lindheimer collections is presented here as an appendix. Measurements of specimens have been made on dried material except for the flowers, which were examined after being boiled. Voucher specimens for pollen and chromosome studies are deposited at the Kriebel Herbarium, Purdue University (PUL). Synonyms and descriptions refer primarily to the taxa as represented in the U. S., and do not necessarily apply to the genus as a whole.

TRAGIA L. Sp. Pl. **2:** 980. 1753; Gen. Pl. ed. 5, 421. 1754.

Perennial herbs, sometimes becoming suffrutescent, erect or decumbent to trailing or twining. Stems solitary to many from the woody crown of the taproot, alternately branched; pubescence of stiff stinging hairs intermingled with soft spreading hairs. Leaves alternate, petiolate or sessile; margins entire to serrate, coarsely toothed to divided; stipules lanceolate, acute, entire, ciliate, usually persistent. Plants monoecious; inflorescences [in most U. S. taxa] opposite the leaves at the upper nodes (actually terminal, but soon surpassed by the branch from the axil of the subtending leaf); racemes androgynous, the lower 1 (2) flowers pistillate, the remaining 2-20+ staminate; individual flowers bracteolate. Flowers apetalous; calyx-lobes 3-6; disk absent in the the flowers of both sexes. Staminate flowers pedicellate, abscission zone below the middle of the pedicel, the basal portion persistent; stamens 2-6 (8) [more in some extralimital taxa]; filaments connate at least at the base, anthers free; pistillode small. Pistillate flowers pedicellate, abscission zone below the middle of the pedicel, the entire structure with the calyx and columella usually persistent; staminodia absent; ovary usually

of 3 carpels, subglobose, hispid to densely hispid with stiff stinging hairs; ovules solitary in each locule, anatropous, with two integuments, obturator penetrating into the exostome in contact with the nucellus; styles 3, spreading or coiling outward at anthesis, united at the base and up to 1/2 or more their length, stigmas smooth or papillate. Fruit an explosively dehiscent capsule, the cocci separating from a persistent columella; columella with 3 interlocular points apically. Seeds one per locule; seed coat dry, crustaceous, smooth or slightly rough, brownish black or with a tawny mottling, ecaruncu-late; endosperm whitish; embryo straight, cotyledons foliaceous and considerably broader than the terete radicle.

KEY TO THE TAXA

A. Stamens 3-4 (rarely 5); calyx-lobes of staminate flowers usually 3, sometimes 4 (rarely 5) ..... Section *Tragia*
B. Stamens 2; calyx-lobes of staminate flowers usually 4 or 5 (rarely 6) ..... Section *Leptobotrys*

Section TRAGIA

1. Leaf blades undivided ..... (2)
1. Leaf blades 3-divided ..... 10. *T. laciniata*
2. Inflorescence without conspicuous stalked glandular hairs .... (3)
2. Inflorescence with conspicuous stalked glandular hairs ..... 1. *T. glanduligera*
3. Filaments of the stamens connate only at the base ..... (4)
3. Filaments of stamens connate 1/3 — 1/2 or more their length; leaf blades deeply and sharply toothed, cuneate at the base .... 11. *T. nigricans*
4. Persistent base of the staminate pedicel usually conspicuously shorter than the subtending bract ..... (5)
4. Persistent base of the staminate pedicel usually almost equalling in length or exceeding the subtending bract; stigmatic surfaces conspicuously papillate; ovary densely pubescent with stinging hairs ..... 3. *T. urticifolia*
5. Calyx-lobes of the pistillate flower shorter than the gynoecium ..... (6)
5. Calyx-lobes of the pistillate flower longer than the gynoecium; bracts of the staminate flowers strikingly long, (1-) 2 mm; staminate flowers 14-75 per inflorescence .... 4. *T. betonicifolia*
6. Leaf blades rounded to acute, scarcely acuminate, not broadly ovate with a deeply cordate base; seeds less than 4 mm long; plants twining or not ..... (7)
6. Leaf blades broadly ovate, more than half as long as broad, acuminate, deeply cordate at the base; seeds more than 4 mm long; plants always twining ..... 2. *T. cordata*
7. Leaf blades ovate to triangular or lanceolate, the broader ones more or less cordate to truncate at base ..... (8)

7. Leaf blades suborbicular to oblong, truncate or rounded at the base; stigmatic surfaces only slightly papillate; plants never twining (restricted to extreme southern Florida) .... 9. *T. saxicola*
8. Stigmatic surfaces distinctly papillate, styles connate only at the base or slightly higher; leaf blades broadly triangular to ovate ..... (9)
8. Stigmatic surfaces not or scarcely papillate (slightly so in aberrant specimens with narrowly lanceolate leaf-blades); styles connate 1/3 to 1/2 their length and usually terminating in slender, recurved tips; leaf blades usually 2-4 times as long as broad ..... 7. *T. ramosa*
9. Plants not densely pubescent on the stem and leaves ..... (10)
9. Plants copiously to densely pubescent, especially on young stems, the entire plant having a greyish-green cast; leaf blades crenate to serrate or dentate, bases truncate to sagittate; ovary very densely pubescent with stinging hairs .. 8. *T. amblyodonta*
10. Leaf blades coarsely serrate-dentate; staminate calyx often reddish; staminate flowers 8-35 per inflorescence; ovary pubescent with stinging hairs (but usually not very densely); fruits monomorphic (all wingless and 3-seeded); plants erect to decumbent ..... 6. *T. nepetifolia*
10. Leaf blades serrate; staminate calyx never reddish; staminate flowers 3-6 (-10) per inflorescence; ovary densely pubescent with stinging hairs; fruits usually dimorphic, either 3-seeded and wingless or 1-seeded and crested or winged; plants very often twining ..... 5. *T. brevispica*

Section Leptobotrys

1. Leaf blades blunt-toothed or lobed, bases of lower leaves truncate; seeds 4.0-4.5 mm long; inflorescences opposite the leaves throughout. ..... 12. *T. smallii*
1. Leaf blades entire, blunt-toothed, or lobed, cuneate at the base; seeds 3.0-4.0 mm long; inflorescences terminating leafy lateral branches, opposite the leaves only toward the tip of the main stem. ..... 13. *T. urens*

Section 1. Tragia

Sect. *Eutragia* Muell. Arg. Linnaea 34: 182. 1865; DC. Prodr. 15 **(2):** 932. 1866.

Perennial herbs, erect, decumbent, or twining; stems and foliage with more or less severely stinging hairs; leaves serrate or dentate, or sometimes deeply lobed or divided; inflorescences opposite the leaves; female flowers 1 or 2 per raceme; staminate flower with 3 or 4 (rarely 5) calyx-lobes; stamens 3-6, filaments more or less cylindrical, somewhat thickened, free or connate; pollen grains distinctly colpate; pistillode subglobose; pistillate flower with 6 (very rarely 5)

calyx-lobes; styles free or connate below, smooth or papillate; seeds 2-5.5 mm long.

LECTOTYPE: *Tragia volubilis* L. (designated by Britton and Wilson, Sci. Surv. Porto Rico 5: 491-492. 1924).

This group of about 30 species almost equally divided between North America and South America is here construed nearly as defined by Pax and Hoffmann (1919), except that *T. urens* and *T. smallii* are removed to sect. *Leptobotrys*, while *T. ramosa* and *T. brevispica* are transferred here from sect. *Leucandra*. It seems probable that additional neotropical species of sect. *Leucandra* (those with a low stamen number) will be transferred to sect. *Tragia* when a more thorough study is made.

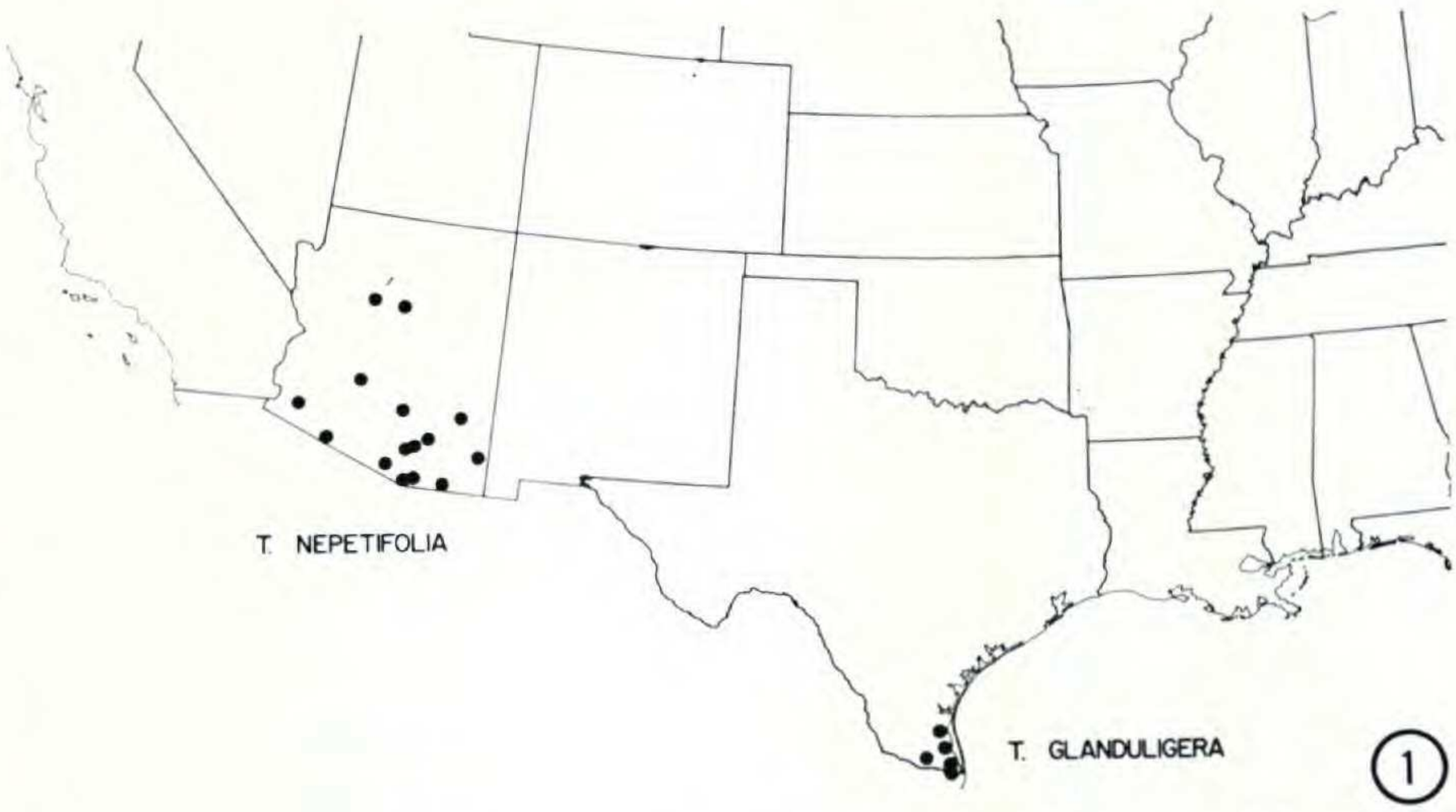
The more or less weedy 'noseburn' species placed together in *T. nepetifolia* by Johnston (1962) are here distributed into species 5-8; *T. betonicifolia*, although treated by Shinners (1958) as a variety of *T. urticifolia*, has often been mistaken for *T. ramosa* and may be regarded as a peripheral member of the 'noseburn' group. At least the first two species, *T. glanduligera* and *T. cordata*, appear to be more closely related to extra-limital taxa than to any U. S. species; in an eventual revision of all of the taxa of sect. *Tragia* they would therefore probably go into separate subsections or series from the remainder (species 3-11).

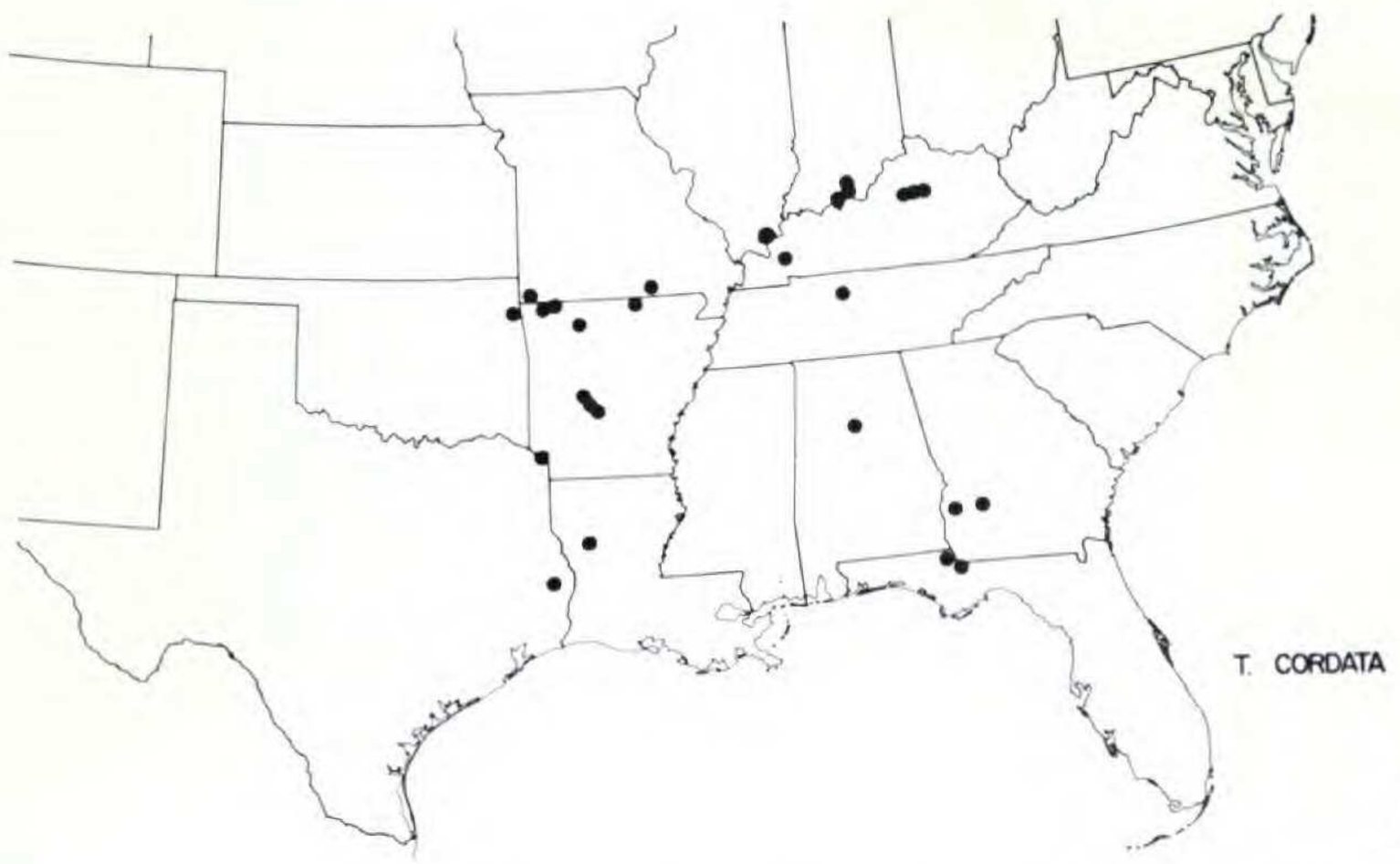
1. **Tragia glanduligera** Pax & Hoffm. Pflanzenreich IV. 147. IX [Heft 68]: 55. 1919. (Fig. 17)

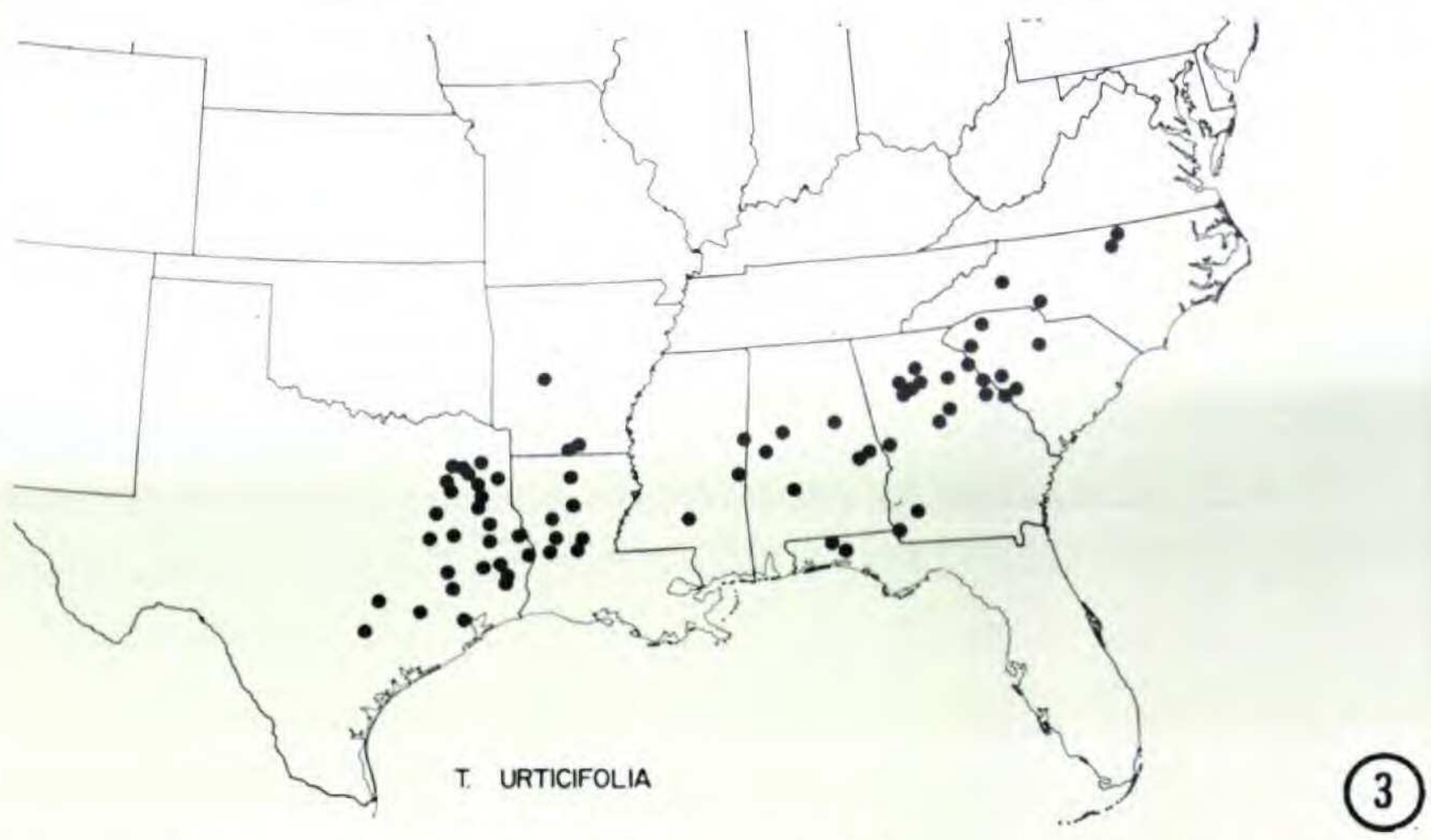
LECTOTYPE: Yucatan, *Gaumer 731* (GH!; isotypes F, MO!).

Stems few to many from the crown of the woody taproot, 1-2 mm in diameter near the base, up to a meter or more long, green to purplish-green, many-branched, trailing and twining; upper internodes 12-35 mm long, lower internodes 20-35 mm long. Leaf blades elliptic to ovate, 2.5-4.0 cm long, 1.5-2.0 cm broad, apically acute to acuminate, basally truncate to cordate, margins crenate to serrate, thin, green, pubescent, ciliate; petioles 6-22 mm long; stipules lanceolate to narrowly ovate, entire, 1.5-4.5 mm long, 0.5-1.2 mm broad at the base, persistent, ciliate, abaxially pubescent. Racemes with the lowermost 1 (2) nodes pistillate, the remaining 10-30 nodes staminate; bracts of the pistillate flowers lanceolate, ca. 0.9-2.0 mm long, ciliate, acute,

Fig. 17. Habit, *Tragia glanduligera* (*M. C. Johnston 542235*).







Map 1. Distribution of *Tragia glanduligera* and *Tragia nepetifolia.*

Map 2. Distribution of *Tragia cordata.*

Map 3. Distribution of *Tragia urticifolia.*

entire or three-lobed, abaxially sparsely pubescent; bracts of the staminate flowers lanceolate, subcucullate, ca. 0.5-1.5 mm long, pubescent, entire. Glandular hairs present over entire inflorescence. Staminate flowers: pedicels slender, 1-2.0 mm long, lower persistent part ca. 0.3-0.7 mm long; calyx-lobes 3, broadly oblanceolate to obovate, 0.7-1.2 mm long, abaxially pubescent, entire, spreading to reflexed at anthesis; stamens 3; filaments thickened and fleshy, 0.2-0.4 mm long, connate basally. Pistillate flowers: pedicels 1.0-2.3 mm long, becoming 3-7 mm in fruit; calyx-lobes 6, lanceolate to narrowly ovate, 0.7-1.5 mm long at anthesis, 1.2-2.3 mm long in fruit, acute, entire, ciliate, abaxially sparsely pubescent; styles connate about 1/3 their length, stigmatic surfaces papillate. Fruit 2-2.5 mm long, 4-5 mm broad; columella 1.5-2 mm long; seeds nearly spherical, 1.9-2.2 mm long, brownish-black when mature.

DISTRIBUTION: restricted in the U. S. to extreme southern Texas in dry sandy soil (Map 1).

REPRESENTATIVE SPECIMENS: — TEXAS: CAMERON CO., Las Palmas Plantation ca. 4 mi SW of Brownsville in a palm grove, *Correll 14848* (LL); Resaca del Rancho Viejo, *Cory 51454* (NY, SMU); 2.4 mi N of Lozano, *Johnston 2758* (SMU); 3 mi east of Harlingen near Arroyo Colorado, *Johnston 3640* (TEX); Camp Perry (Boy Scout Camp), *Johnston 542235* (TEX); palm grove S of Brownsville, *Lundell & Lundell 10002* (SMU); N of Los Fresnos in mesquite brush, *Lundell & Lundell 10665* (LL, SMU, TEX); Brownsville, *Tharp 1870* (TEX). HIDALGO CO., La Joya, *Walker s.n.* (2/II/1942) (TEX). KENEDY CO., Norias Division of King Ranch a few miles W of La Calandria, *Johnston 541069* (SMU). WILLACY CO., *Tharp s.n.* (26/VI/1941) (TEX).

Pax and Hoffmann (op. cit. 56) cited collections of Berlandier, Gaumer, and Valdez when describing this species. The Berlandier specimens are somewhat atypical and it is not certain that they are conspecific. The Valdez collection is perhaps equally representative, but as the Gaumer collection is more widely distributed it has been chosen as the lectotype.

Tragia glanduligera is a primarily Mexican species of the Gulf coastal lowlands between Yucatan and the Rio Grande, crossing into Texas only in four of the southernmost counties. Specimens from further north which have been reported as *T. glanduligera* (Jones, Rowell, & Johnston

Fig. 18. Habit, *Tragia cordata* (*M. E. Wharton 9369*).

1961) actually belong to *T. brevispica*, a species which clearly differs in its non-glandular inflorescence, more sharply toothed leaves, and larger dimorphic fruits. The glandular inflorescence and diminutive seeds (smaller than those of any other U. S. species) easily distinguish *T. glanduligera* from other taxa occurring in Texas.

2. **Tragia cordata** Michx. Fl. Bor. Amer. **2:** 176. 1803. (Fig. 18)

TYPE: Kentucky, 'entre Danville et Beards' town', *Michaux* (P!).

Tragia macrocarpa Willd. Spec. Pl. **4:** 323. 1805; based on the same type.

Tragia Michauxii Baill. Étud. Gén. Euphorb. 460. 1858; based on the same type.

Stems solitary or few from the crown of the woody taproot, 1.5-3 mm in diameter near the base, up to 1.5 m or more long, green to yellowish-green, few to many-branched, trailing and twining; upper internodes 2-7.5 cm long, lower internodes 3-10 cm long. Leaf blades broadly ovate, 4.5-13 cm long, 3.6-10 cm broad, apically acuminate, basally cordate, margins coarsely serrate, thick, green, pubescent, ciliate; petioles 1.5-8.5 cm long; stipules lanceolate to narrowly ovate, entire, 1.8-10 mm long, 0.4-2.1 mm broad at the base, persistent, ciliate, abaxially sparsely pubescent. Racemes with the single lowermost node pistillate, the remaining 20-60 nodes staminate; bracts of the pistillate flowers lanceolate, ca. 1.6-2 mm long, ciliate, acute, entire or three-lobed, abaxially sparsely pubescent; bracts of the staminate flowers lanceolate, subcucullate, ca. 1.5-2 mm long, pubescent, entire. Staminate flowers: pedicels slender, 1.5-2.2 mm long, lower persistent part ca. 0.7-1 mm long; calyx-lobes 3(91%) (4), oblanceolate to narrowly obovate, 0.7-1.5 mm long, abaxially pubescent, entire, spreading to reflexed at anthesis; stamens 3 (96%) (4); filaments thickened and fleshy, 0.2-0.5 mm long, connate basally. Pistillate flowers: pedicels 1-1.5 mm long, becoming 2.5-3 mm in fruit; calyx-lobes 6 (96%) (-7), elliptic to ovate, 1.5-2 mm long at anthesis, 2-3 mm long in fruit, acuminate, entire, ciliate, abaxially pubescent; styles connate 1/4-1/3 their length, stigmatic surfaces papillate. Fruit 5-7 mm long, 11-13 mm broad; columella 2.2-3.4 mm long; seeds nearly spherical, 4.3-5.3 mm long, brownish-black with a tawny mottling when mature.

DISTRIBUTION: Indiana to Missouri and east Texas more or less following the eastern deciduous forests (Map 2).

REPRESENTATIVE SPECIMENS: — ALABAMA: JEFFERSON CO., Birmingham, *Earle 2074* (NY). ARKANSAS: HOT SPRINGS CO., Magnet Cove, *Demaree 22407* (SMU). FLORIDA: JACKSON CO., Florida

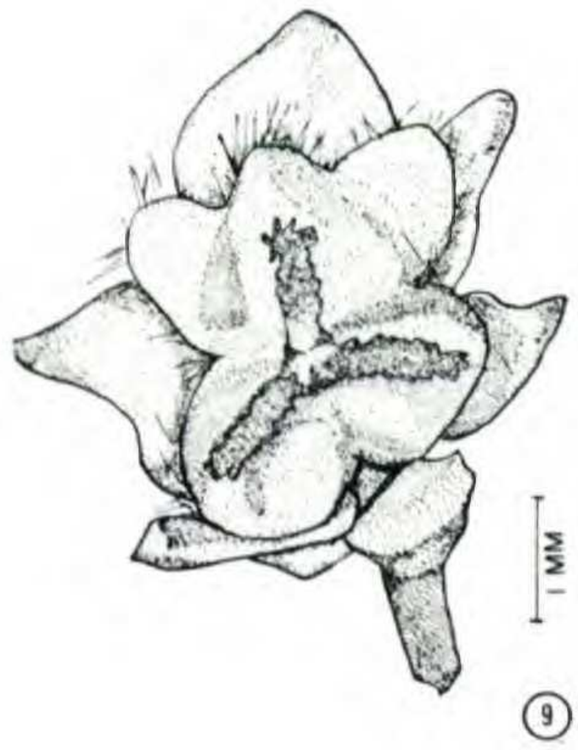
Caverns State Park, *Beck 225* (FLAS, GA). GEORGIA: LEE CO., along Fowlton Creek near Armena, *Thorne & Muenscher 8413* (GA). ILLINOIS: POPE CO., Golconda, *Forbes* (F). INDIANA: CRAWFORD CO., roadside 1/4 mi W of Leavenworth, *Deam 18583* (NY). KENTUCKY: LYON CO., Skinframe Creek, *Eggleston s.n.* (14/VI/1909) (NY). MISSOURI: MCDONALD CO., rocky ground, uncommon, *Bush s.n.* (24/VII/1893) (NY). OKLAHOMA: DELAWARE CO., Little Kansas, DEMAREE *22407* (SMU). TENNESSEE: DAVIDSON CO., woods near Nashville, *Gattinger 2518* (KANU, NY, PH, SMU, UARK). TEXAS: BOWIE CO., 3 mi N of Texarkana, *Correll 15249* (LL).

Tragia cordata, which attains the northernmost latitude of any species in the genus, is not easily confused with any of the other U. S. taxa: it is set apart by the vining habit, large deeply cordate leaves, and large fruits and seeds. Its closest affinities would appear to be with Mexican species such as *T. affinis* Rob. & Greenm.

3. **Tragia urticifolia** Michx. Fl. Bor. Amer. **2:** 176. 1803. (Figs. 6, 14, 19)

TYPE: Georgia [ex Michaux, loc. cit.], *Michaux* (P!).

Stems solitary or few from the crown of the woody taproot, 3-4 mm in diameter near the base, 25-65 cm tall, green to yellowish-green, simple to few-branched, erect to decumbent; upper internodes 8-30 mm long, lower internodes 12-60 mm long. Leaf blades triangular-lanceolate to narrowly ovate, 2.7-6.7 cm long, 0.9-3.2 cm broad, apically acute, basally cordate to truncate, petioles 3-11(-17) mm long; stipules lanceolate to narrowly cordate, entire, 2-5 mm long, 0.6-1.6 mm broad at the base, persistent, ciliate, abaxially pubescent. Racemes with the lowermost 1 (2) nodes pistillate, the remaining 11-40 nodes staminate; bracts of the pistillate flowers lanceolate, ca. 1-1.5 mm long, ciliate, acute, entire or three-lobed, glabrous or abaxially sparsely pubescent; bracts of the staminate flowers lanceolate, subcucullate, ca. 0.7-1.5 mm long, pubescent, entire. Staminate flowers: pedicels slender, 1.5-2 mm long, lower persistent part ca. 1-1.8 mm long, as long as or exceeding the bract; calyx-lobes 3 (93%) (4), oblanceolate to narrowly ovate, 1.2-2.1 mm long, abaxially pubescent, entire, spreading to reflexed at anthesis; stamens 3; filaments thickened and fleshy, 0.3-0.8 mm long, connate basally. Pistillate flowers: pedicels 0.5-1 mm long, becoming 3-4 mm in fruit; calyx-lobes (5) 6 (86%), lanceolate to ovate, 1.3-2.2 mm long at anthesis, 2-3 mm long in fruit, acute, entire, ciliate, rarely abaxially pubescent; styles connate 1/3-1/2 their length, stigmatic surfaces



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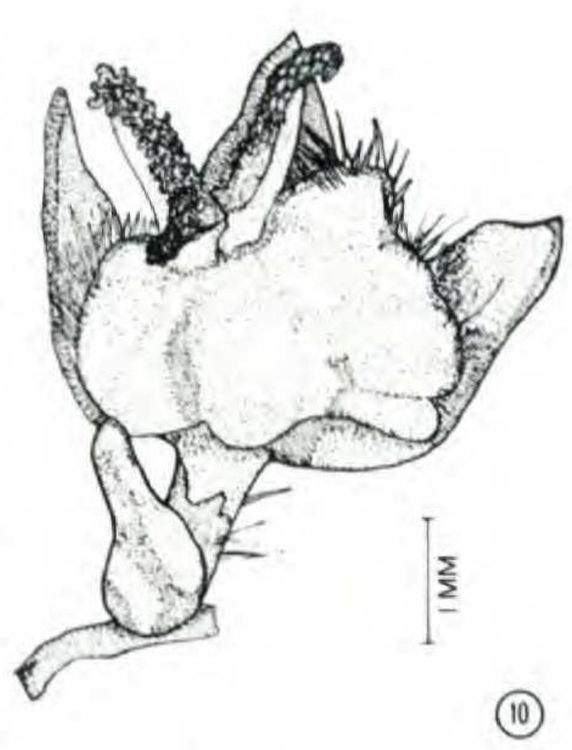

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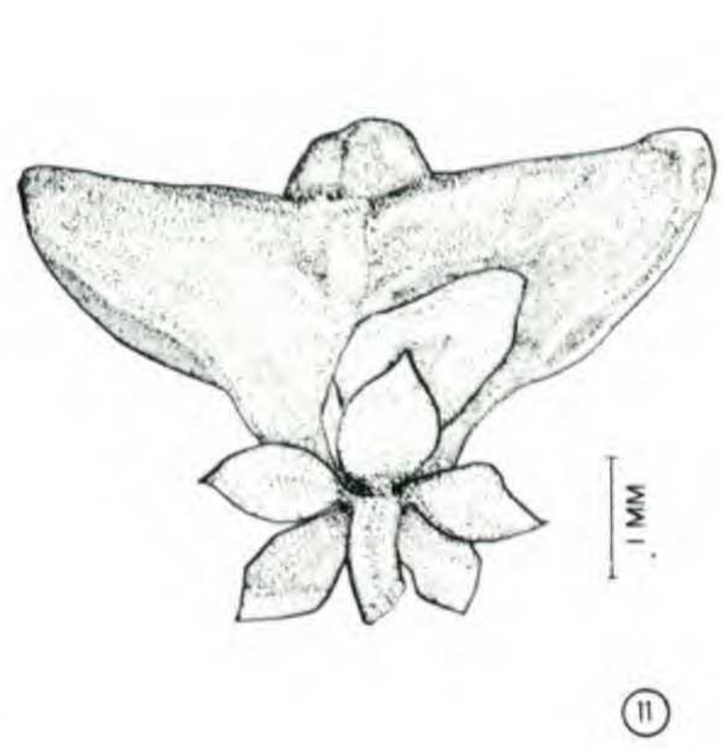

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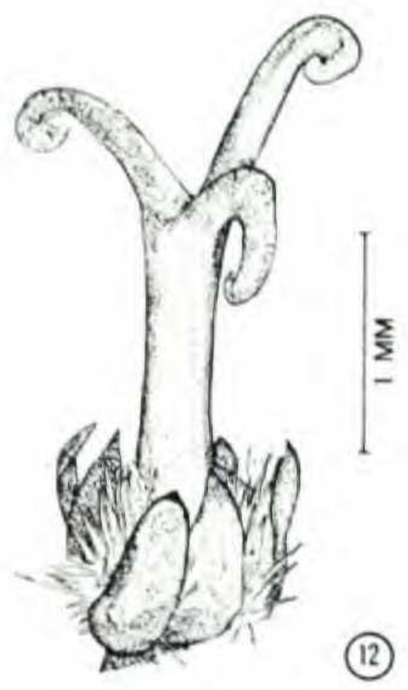

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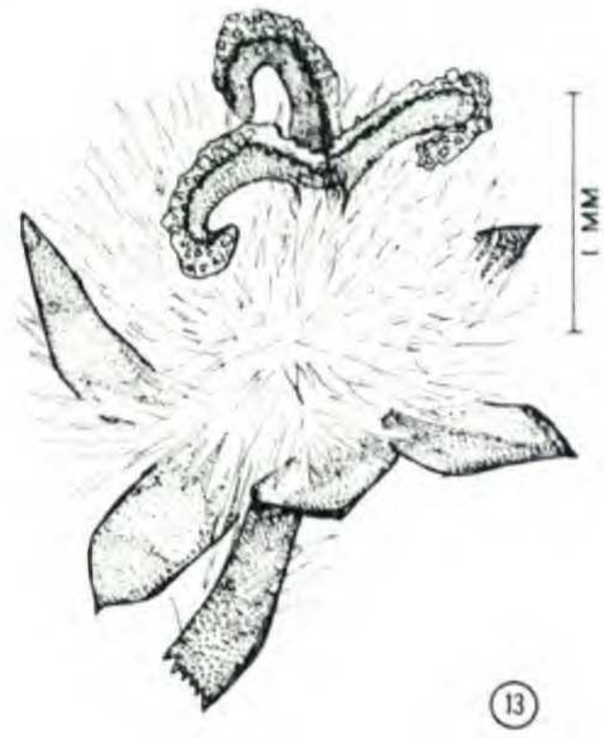

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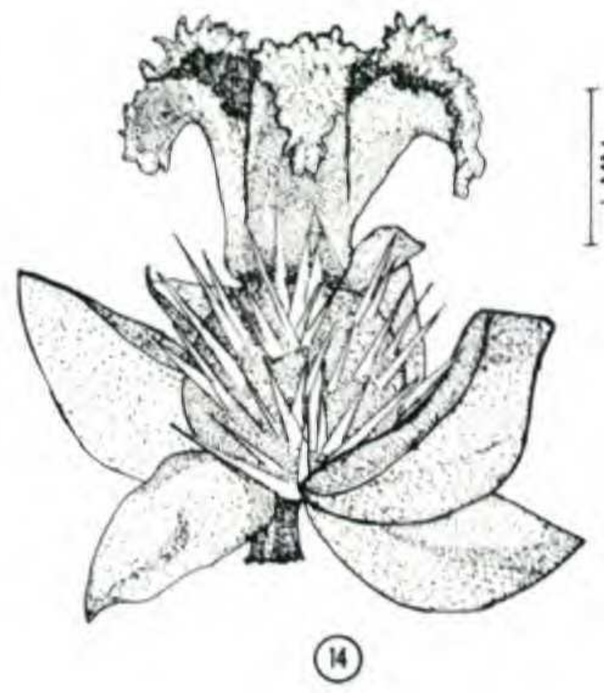

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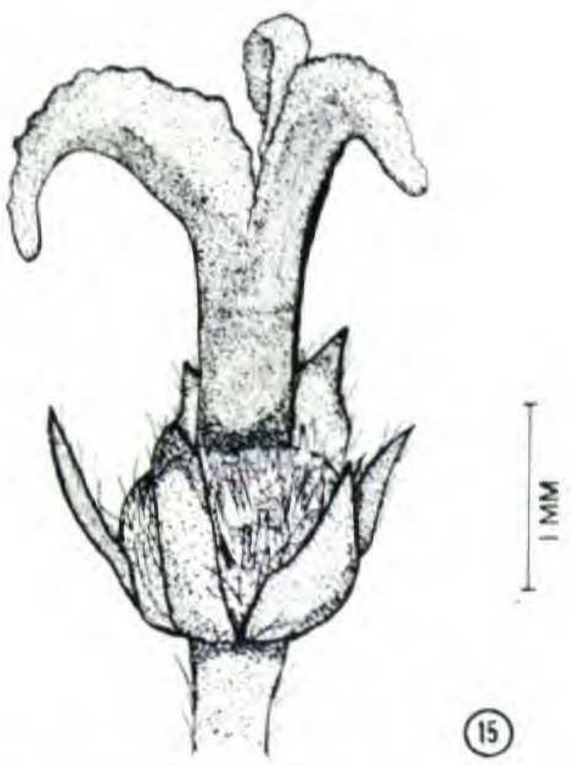

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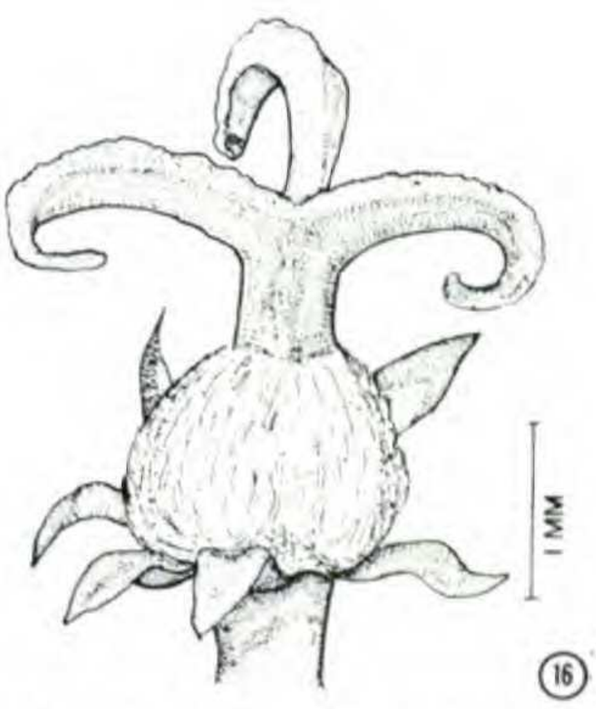

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Figs. 9 and 10. Early stage in development of winged fruit, *Tragia brevispica* (*K. & L. Miller 1076*).

Fig. 11. Mature one-seeded winged fruit, *Tragia brevispica* (*K. & L. Miller 1076*).

Fig. 12. Pistillate flower, *Tragia ramosa* (*K. & L. Miller 1341*).

Fig. 13. Pistillate flower, *Tragia amblyodonta* (*K. & L. Miller 1178*).

Fig. 14. Pistillate flower, *Tragia urticifolia* (*K. & L. Miller 848*).

Fig. 15. Pistillate flower, *Tragia smallii* (*K. & L. Miller 865*).

Fig. 16. Pistillate flower, *Tragia urens* (*K. & L. Miller 776*).

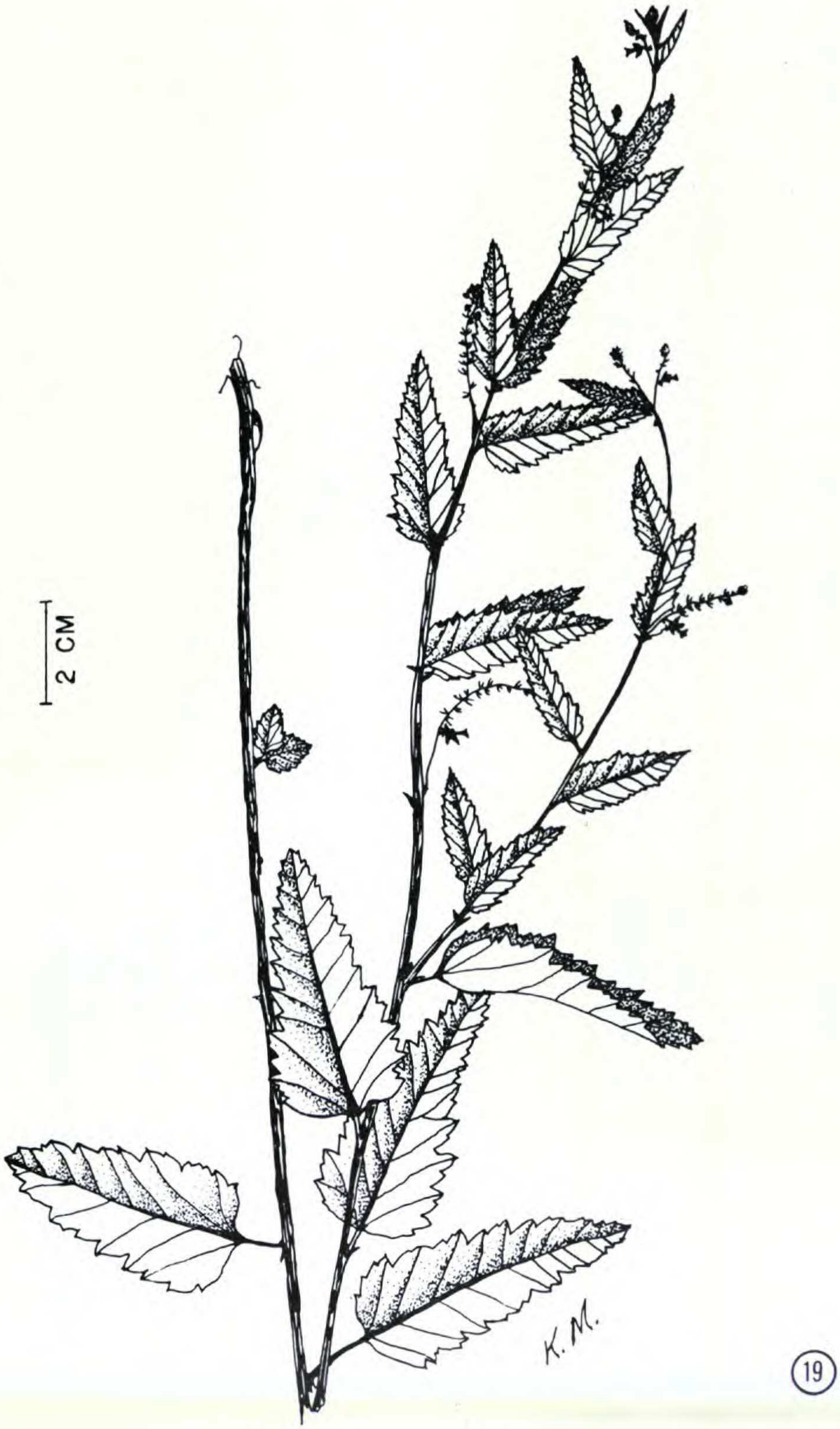


Fig. 19. Habit, *Tragia urticifolia* (*K. & L. Miller 848*).

very papillate. Fruit 3.5-4.5 mm long, 7-8 mm wide; columella 2-2.8 mm long; seeds nearly spherical, 3-4 mm long, brownish-black when mature.

DISTRIBUTION: North Carolina south to northern Florida and west to Texas and Arkansas, typically in dry sandy soil in open woods and fields (Map 3).

REPRESENTATIVE SPECIMENS: — ALABAMA: TALLADEGA CO., Childersberg, *Hood 4680* (FLAS). ARKANSAS: GARLAND CO., near Hot Springs, *Palmer 29069* (UARK). FLORIDA: OKALOOSA CO., Crestview, *West s.n.* (27/IX/1950) (FLAS). GEORGIA: BAKER CO., bank of Cooleewahee Creek at Newton, *Thorne 5695* (GA, IA). LOUISIANA: WINN PARISH, 10 mi W of Winnfield, *Webster & Wilbur 3266* (NCSC, SMU). MISSISSIPPI: LAUDERDALE CO., 18 mi SW of Quitman on Rt. 18, *Miller & Miller 872* (PUL). NORTH CAROLINA: GRANVILLE CO., 0.5 mi W and 2 mi N of Hester, *Ahles & Leisner 17499* (TEX). SOUTH CAROLINA: EDGEFIELD CO., ca. 3 mi. W of Owdoms, *Miller & Miller 844* (PUL). TEXAS: BASTROP CO., Bastrop State Park, *Correll & Johnston 17433* (LL): SALINE CO., Redhills Lake, *Miller & Miller 915* (PUL).

Tragia urticifolia is a very distinct species although it has been misinterpreted by some writers of floras. Gleason (1952), in 'Britton & Brown's New Illustrated Flora', reversed the distinction between *T. urticifolia* and *T. nepetifolia* when he stated that '*Tragia nepetifolia* is similar in habit but the persistent pedicel-base of the staminate flowers is as long as the bract, the short filaments are as wide as the anthers, and the styles are scarcely connate.' These statements pertain to *T. urticifolia* and not to *T. nepetifolia*, as he intended. Gleason also attributed a much wider distribution to *T. urticifolia* than actually exists.

The only species which is at all close to *T. urticifolia* is *T. betonicifolia*, which is largely allopatric, overlapping with *T. urticifolia* only in eastern Texas and in Arkansas. Although *T. betonicifolia* seems sufficiently distinct to be regarded as a separate species (as discussed below), it doubtless may be regarded as the western vicariant of *T. urticifolia*.

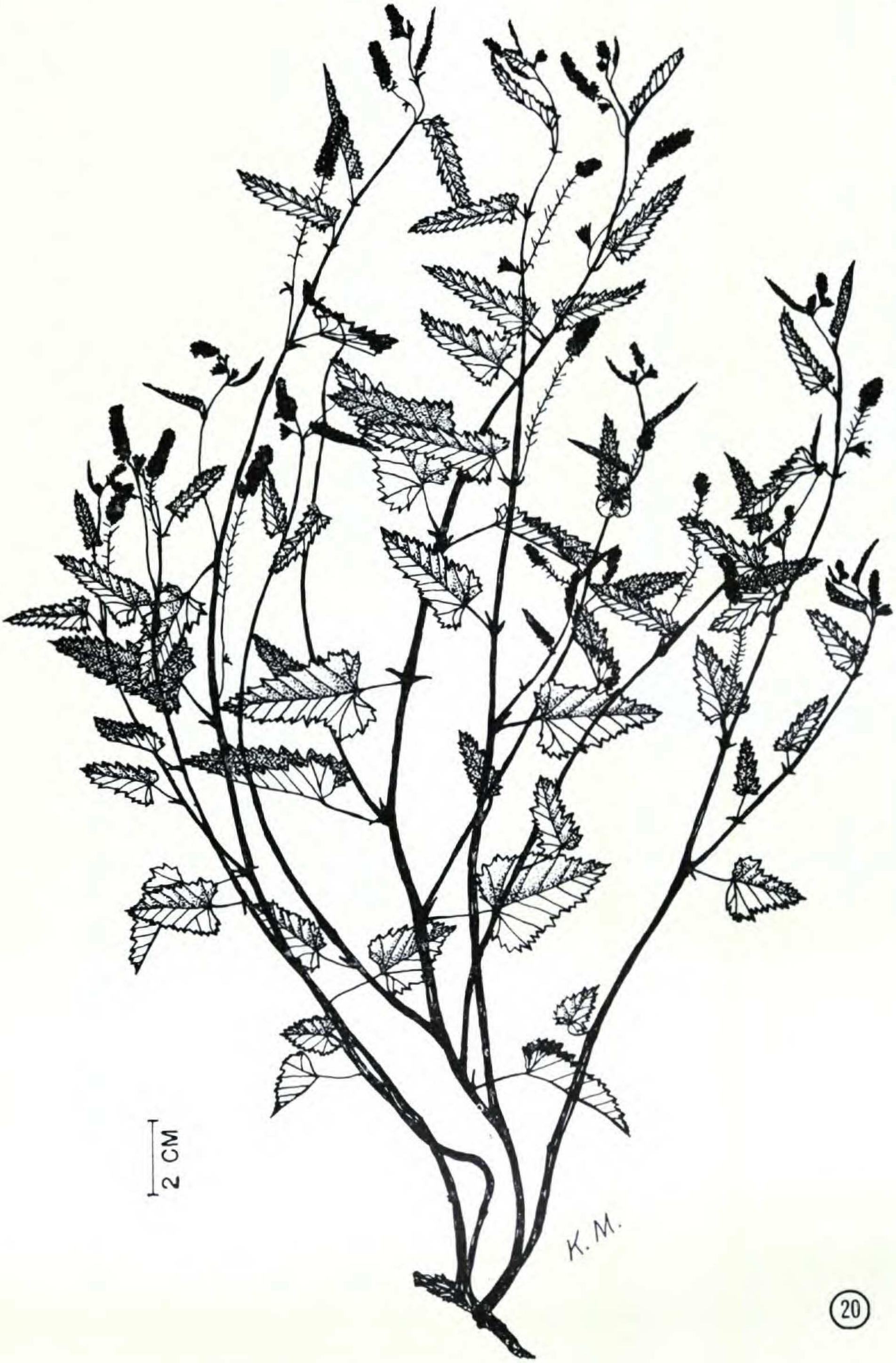


Fig. 20. Habit, *Tragia betonicifolia* (*J. Hancin 1311*).

4. **Tragia betonicifolia** Nutt. Trans. Amer. Phil. Soc. (n.s.) **5:** 173. 1837. (Fig. 20)

TYPE: 'Arkansas', Red River, *Nuttall* (BM!).

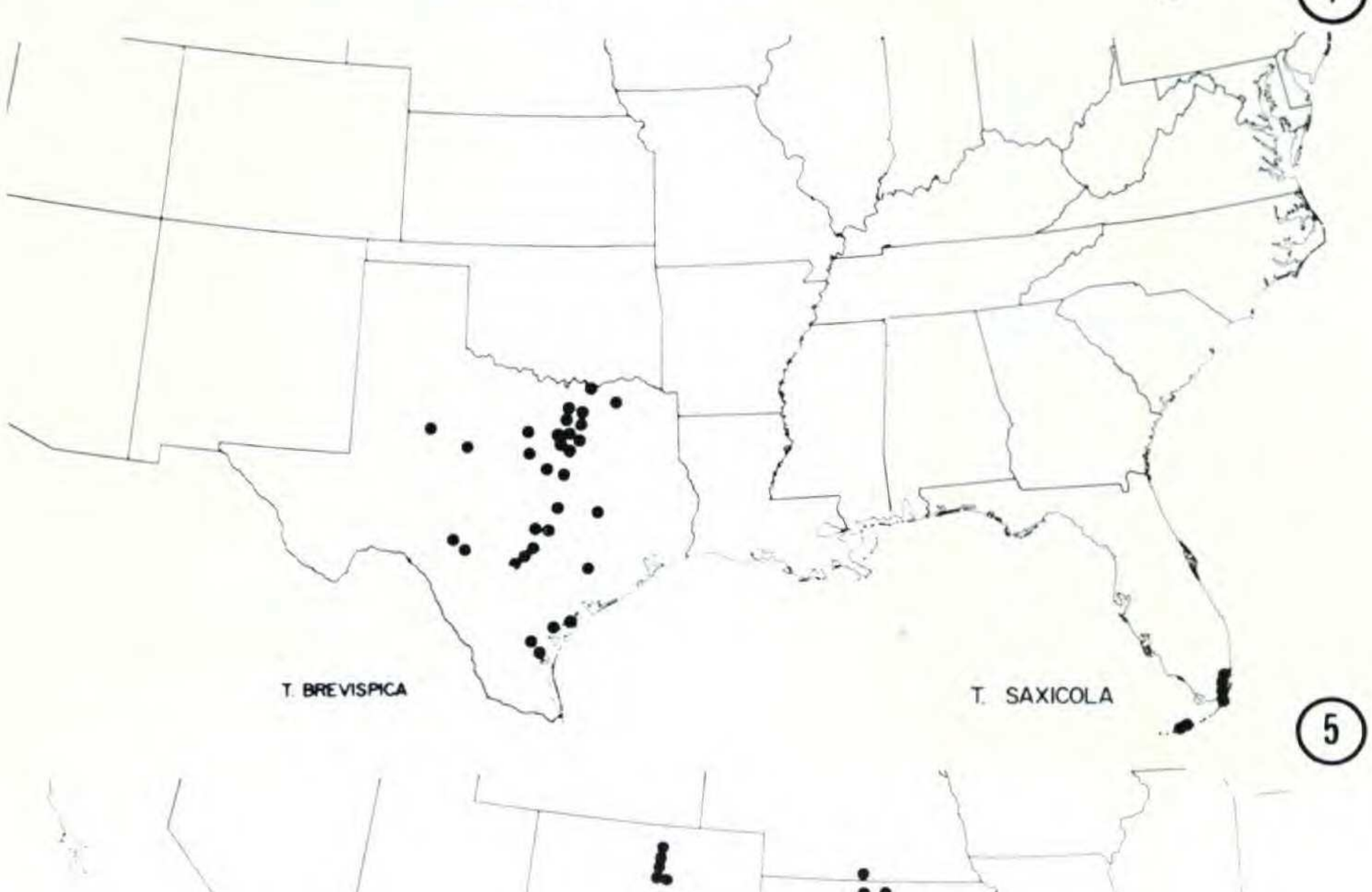
Tragia urticifolia var. *texana* Shinners, Field & Lab. **19:** 183. 1951.

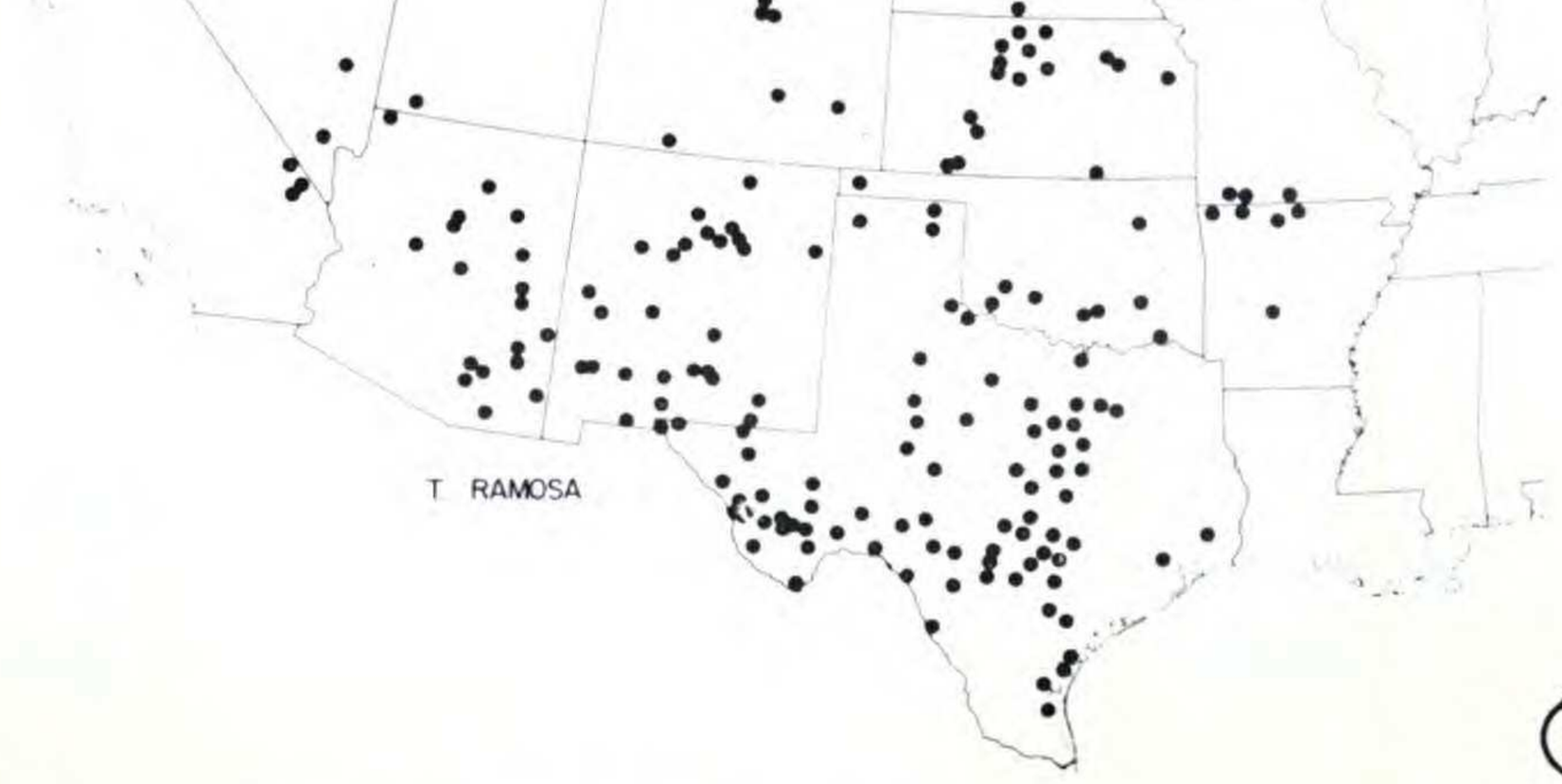
TYPE: 6 mi NW of Grapevine, Tarrant Co., Texas, *Shinners 11133* (SMU!)

Stems few to many from the crown of the woody taproot, 1-2.5 mm in diameter near the base, 20-50 cm tall, green to yellowish-green, few-branched to many-branched, erect or decumbent to trailing; upper internodes 10-30 mm long, lower internodes 15-45 mm long. Leaf blades ovate, ovate-lanceolate to triangular-lanceolate, 1.5-5.5 cm long, 0.9-3.5 cm broad, apically acute, basally cordate to truncate, margins sharply serrate, thick, green, pubescent; petioles 0.8-3.5 cm long; stipules ovate to ovate-lanceolate, attenuate, entire 2.5-6 mm long, 0.5-2.5 mm broad at the base, persistent, ciliate, abaxially sparsely pubescent. Racemes with the lowermost 1 (2) nodes pistillate, the remaining 14-75 nodes staminate; bracts of the pistillate flowers lanceolate, ca. 1.5-2 mm long, ciliate, acute, entire or three-lobed, abaxially sparsely pubescent; bracts of the staminate flowers lanceolate, subcucullate, ca. 1-2 mm long, pubescent, entire. Staminate flowers: pedicels slender, 0.7-1 mm long, lower persistent part ca. 0.3-0.6 mm long; calyx-lobes 3 (68%)-4 (26%) (5), oblanceolate to narrowly obovate, 1.2-2.3 mm long, abaxially pubescent, entire, spreading to reflexed at anthesis; stamens 3 (71%)-4 (27%) (5); filaments thickened, 0.4-1 mm long, connate basally. Pistillate flowers: pedicels 0.7-1 mm long, becoming 3-4 mm in fruit; calyx-lobes 6, lanceolate, 1.8-3.0 mm long at anthesis, 3-5 mm long in fruit, acute to attenuate, entire, ciliate, abaxially sparsely pubescent; styles connate only at the base or up to 1/3 their length, stigmatic surfaces papillate. Fruit 4-5 mm long, 7-9 mm broad; columella 2.5-3 mm long; seeds nearly spherical, 3-4 mm long, brownish-black with a tawny mottling when mature.

DISTRIBUTION: open woods, fields, and roadsides, usually on dry sandy soil, Texas north through Oklahoma and Arkansas to Kansas and Missouri (Map 4).

REPRESENTATIVE SPECIMENS: — ARKANSAS: FRANKLIN CO., Horseshoe Mountain (Little Short Mountain), *Iltis & Iltis 5400* (MICH, SMU). RANDOLPH CO., Ravenden Springs, clay thickets, *Demaree 29217* (SMU). KANSAS: MCPHERSON CO., McPherson State Park, *McGregor 10739* (KANU). Ellsworth Co., 1 mi E of Terra Cotta, *McGregor 12396* (KANU). MISSOURI: JASPER CO., near old mines, Webb City, *Demaree 40340* (SMU); 2 mi NE of Webb City, *Miller & Miller 1350* (PUL). OKLAHOMA: ATOKA CO., 10 mi S of Kiowa, *Matlock*





Map 4. Distribution of *Tragia betonicifolia.*
Map 5. Distribution of *Tragia brevispica* and *Tragia saxicola.*
Map 6. Distribution of *Tragia ramosa.*

114 (SMU). JOHNSTON CO., 10 mi S of Tishomingo along Highway 99, *Robbins 3066* (SMU). TEXAS: LEE CO., 2.5 mi SW of Giddings, *Cory 55763* (SMU). TARRANT CO., E of Euless on Bear Creek N of Highway 183, *Whitehouse 16138* (SMU).

Although Shinners described this species as a variety of *T. urticifolia*, it is readily separable from that plant by the length of the bracts subtending the staminate flowers and by the pistillate calyx-lobes. In *T. betonicifolia* the persistent base of the staminate pedicel is greatly exceeded by the subtending bract, whereas in *T. urticifolia* the pedicel base usually equals in length or exceeds the subtending bract. The calyx-lobes of the pistillate flower in *T. betonicifolia* are usually more lanceolate and always longer than those of *T. urticifolia* (and of most related taxa); the entire gynoecium of *T. betonicifolia* is enveloped by the calyx at anthesis, but in *T. urticifolia* and most other U. S. species of *Tragia* the top of the ovary and the styles are protruding at this stage.

Both Fernald (1950) and Gleason (1952) referred the Missouri populations of *T. betonicifolia* and *T. ramosa* to *T. urticifolia*, but the latter species is not known to enter Missouri. The specimens from the New York Botanical Garden designated as having been used for the illustrations in Gleason's manual actually represent two Missouri collections of *T. betonicifolia*.

5. **Tragia brevispica** Engelm. & Gray, Jour. Boston Soc. Nat. Hist. 5: 262. 1845. (Figs. 9-11, 21)[4]

TYPE: Texas, 'Black, clayey soil, in the prairies west of the Brazos.

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4. The typification of *Tragia brevispica* presents unusual intricacies even for this genus, and it is with some reluctance that we have adopted it in place of the name *T. teucriifolia*. Engelmann and Gray, in their original publication, based the name on Lindheimer 307, which according to Blankinship (1907) belongs to Fascicle II of the Lindheimer collections (see the appendix to this paper), made in 1844. The only specimen examined with a label corresponding to the locality data cited by Engelmann and Gray is in the Paris Herbarium, and it seems possible that this sheet was sent on exchange by Gray, who did not bother to retain the original label. The specimens at

Fig. 21. Habit, *Tragia brevispica* (*E. Whitehouse 16302*).

May — July' [1844], *Lindheimer 307* [Fascicle II] (GH, lectotype!; MO, NY, P, SMU, isotypes!)

Tragia teucriifolia Scheele, Linnaea **25**: 586. 1852.

TYPE: Texas, 'am Rande von Gebüsch und im Pflanzengestrüpp an sonnigen Stellen bei Neubraunfels, Julio — Septbr., 1846', *Lindheimer 522* [Fascicle III] (GH, MO, TEX!).

Tragia nepetifolia δteucriifolia (Scheele) Muell. Arg. in DC. Prodr. **15(2)**: 934. 1866.

Stems solitary or few from the crown of the woody taproot, 1-2 mm in diameter near the base, 20 cm tall up to a meter or more long, green to yellowish-green, few to many-branched, erect to trailing and twining; upper internodes 10-20 mm long, lower internodes 20-35 mm long. Leaf blades broadly triangular, 1.8-5 cm long, 1.3-3 cm broad, apically acute, basally truncate to shallowly cordate, margins finely and shallowly serrate, thin, green, pubescent, ciliate; petioles 7-30 mm long; stipules lanceolate to ovate, entire, 1.4-3 mm long, 0.7-1.4 mm broad at the base, persistent, ciliate. Racemes with the lowermost node pistillate, the remaining 3-6(10) nodes staminate; bracts of the pistillate flowers lanceolate, ca. 1-1.4 mm long, ciliate, acute, entire or three-lobed; bracts of the staminate flowers lanceolate, subcucullate, ca. 1-1.8 mm long, ciliate, entire. Staminate flowers: pedicels slender, 1-1.5 mm long, lower persistent part ca. 0.4-0.7 mm long; calyx-lobes 3 (25%)-4 (70%) (5), ovate to obovate, 1-1.5 mm long, abaxially pubescent, entire, spreading to reflexed at anthesis; stamens 3 (31%), 4 (54%)-5 (15%); filaments slender, thickened and fleshy, 0.3-0.6 mm long, connate basally. Pistillate flowers: pedicels 0.5-1 mm long, becoming 2-4 mm in fruit; calyx-lobes 6, ovate, 1.3-2.0 mm long at anthesis, 1.8-3.5 mm long in fruit, acute, entire, ciliate or abaxially pubescent; styles connate only at the base or up to 1/3 their length; stigmatic surfaces papillate. Fruits often of two kinds on the same plant; some 3-seeded, typically dehiscing, 3.5-4 mm long, 6.5-7.0 mm broad; other fruits with 1-3 distinct wings, more or less indehiscent; columella 1.8-2.8 mm long; seeds nearly spherical, 2.8-3.8 mm long, brownish-black with a tawny mottling when mature.

DISTRIBUTION: limestone regions of central Texas, extending into northern Mexico (Map 5).

Paris, Harvard, Missouri Botanical Garden, and New York herbaria all seem to belong to the same gathering, representing a plant which is more narrow-leaved than other individuals collected by Lindheimer in later years. There are no fruits on any of the sheets of *Lindheimer 307*, and the flowers are not sufficiently characteristic so that we can be absolutely positive of the specific identity of *T. brevispica* with *T. teucriifolia*.

REPRESENTATIVE SPECIMENS: — TEXAS: COLLIN CO., 6 mi S of Frisco on McDonald Farm, *Wagner 114* (SMU). ELLIS CO., along White Rock Creek, 11 mi S of Italy, *Correll & Johnston 17366* (LL). MCLENNAN CO., *Smith 240* (TEX). REAL CO., 4 mi N of Leakey, *Miller & Miller 1165* (PUL). SAN PATRICIO CO., Welder Wildlife Refuge, *Miller & Miller 1076* (PUL). TARRANT CO., Fort Worth, Bluebird Avenue, *Cory 54778* (KANU, LL, SMU). TRAVIS CO., Austin, Albers' herb garden, *Warnock W1076* (TEX); Pecan Springs, E of Austin, *Lundell & Lundell 8939* (LL).

Mueller (1866) treated *T. teucriifolia* as a variety of his all-inclusive *T. nepetifolia*, but may not have examined any specimens of the type collection, as he cited *Lindheimer 307* only under his var. *ramosa*. Johnston (1962) does not even recognize the taxon at the subspecific level. Our own concept, in contrast, is essentially in agreement with that of Pax and Hoffmann (1919), who accepted *T. teucriifolia* as a distinct species and placed it closest to *T. ramosa*. The commonest forms of *T. brevispica* appear very different from *T. ramosa* because of their twining stems, broader rather bluntly toothed leaves, papillate styles, and dimorphic fruits. However, occasional specimens are encountered which are difficult to place in one species or the other. Because of the extraordinary plasticity of *T. ramosa*, it is not easy to exclude the possibility that such 'aberrant' or 'intermediate' specimens may simply be imperfect herbarium samples of that widespread species. On the other hand, *T. brevispica* and *T. ramosa* are widely sympatric over much of central Texas, and it would not be surprising if occasional hybridization occurred. Such specimens as e.g. *Tharp et al. 51-953* from NW Travis County (TEX *89561*) might possibly represent interspecific crosses. Without careful field observations, however, we would not want to positively specify a hybrid origin for any specimens examined in this study.

Despite the confusion of *T. brevispica* with *T. ramosa*, it may actually be more closely related to the Mexican *T. nepetifolia*, which in our area is known only from southern Arizona. The Arizona race of *T. nepetifolia* has leaves and

female flowers rather similar to those of *T. brevispica*, but clearly differs in its reddish male flowers, non-twining habit, and monomorphic fruits. The south Texas and Mexican twining species *T. glanduligera* is not sympatric with *T. brevispica* as far as can be determined from available records, but their ranges approach closely in the Corpus Christi area and it seems possible that they may overlap slightly. However, *T. glanduligera* is certainly not closely related to *T. brevispica*, and is easily distinguished by its glandular inflorescence, more finely toothed and less deeply cordate leaves, and smaller seeds.

The growth habit of *T. brevispica* appears to show considerable lability in response to environmental conditions. Plants growing in open areas are more or less erect (the type collection being of this kind), while those in shade are normally trailing with much longer internodes and broader leaves. Both the erect and trailing forms develop the characteristic winged fruits.

6. **Tragia nepetifolia** Cav. Icones Pl. **6:** 37, pl. 557 fig. 1. 1801. (Fig. 22)

TYPE: Mexico, Hidalgo, 'inter Ixmiquilpan et Zimapan', *Née* (MA, photographs!).

Tragia nepetifolia Σ *genuina* Muell, Arg. in DC. Prodr. **15(2):** 934. 1866.

Stems few to many from the crown of the woody taproot, 1-2 mm in diameter near the base, 15-40 cm tall, green to purplish-green, few to many-branched, erect, decumbent or trailing; upper internodes 10-25 mm long, lower internodes 15-50 mm long. Leaf blades triangular to ovate, 1.8-4 cm long, 0.9-2.7 cm broad, apically acute, basally truncate to cordate, margins irregularly coarsely toothed, thin, green, pubescent, ciliate; petioles 3-25 mm long; stipules lanceolate to narrowly ovate, entire, 2-5 mm long, 0.7-2 mm broad at the base, persistent, ciliate, abaxially pubescent. Racemes with the single lowermost node pistillate, the remaining 8-35 nodes staminate; bracts of the pistillate flowers lanceolate, ca. 1.3-1.6 mm long, ciliate, acute, entire or three-lobed, abaxially sparsely pubescent; bracts of the staminate flowers lanceolate, subcucullate, ca. 1.3-1.6 mm long, pubescent, entire. Staminate flowers: pedicels slender, 1.4-1.7 mm long, lower persistent part ca. 0.5-0.7 mm long; calyx-lobes 3(79%) -4 (21%), elliptic to ovate, 1-2 mm long, glabrous or abaxially pubescent, entire, spreading to reflexed at anthesis; stamens (2) 3(88%)-4

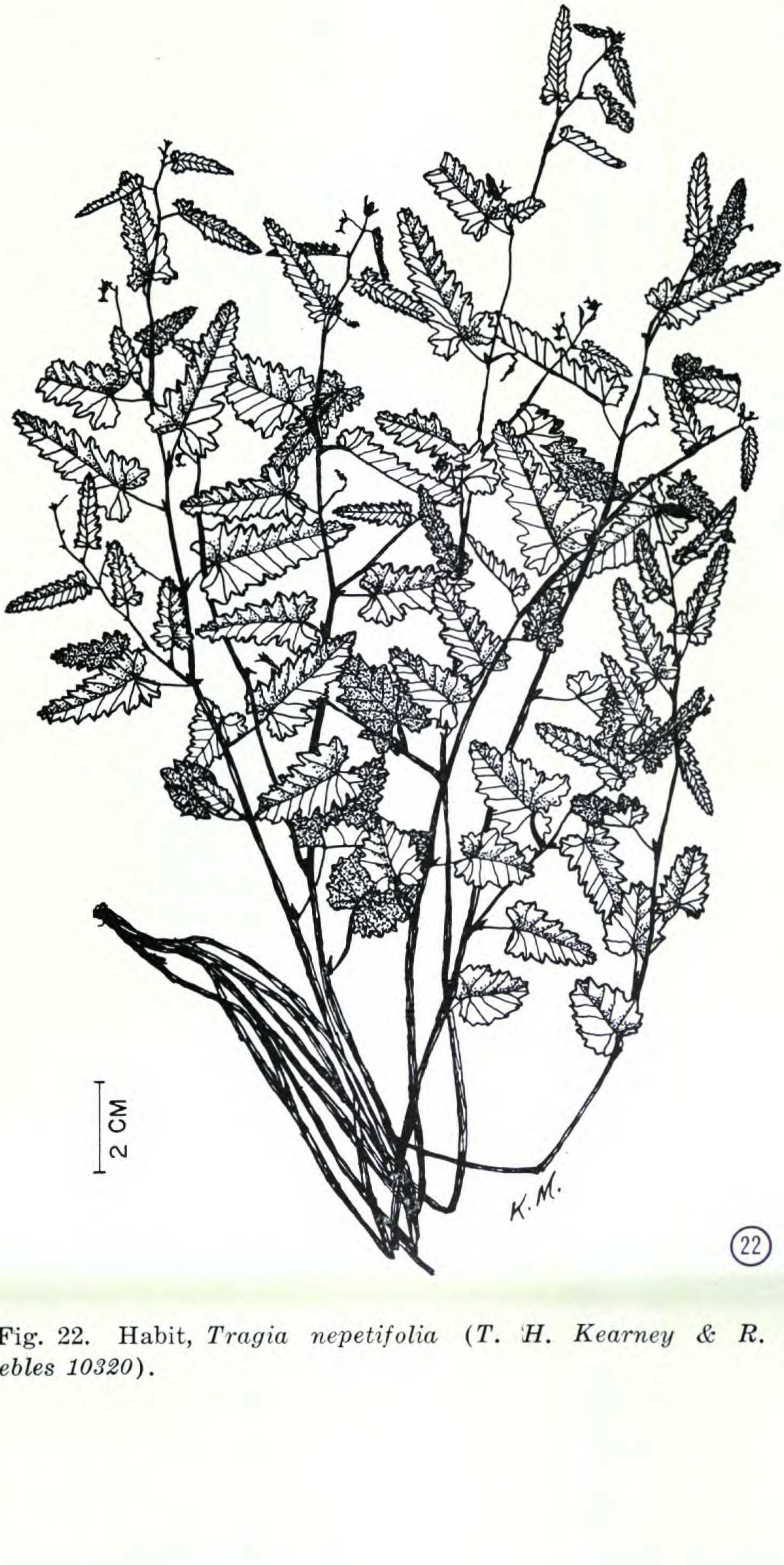

Fig. 22. Habit, *Tragia nepetifolia* (*T. H. Kearney & R. H. Peebles 10320*).

(11%); filaments thickened and fleshy, 0.3-0.6 mm long, connate basally. Pistillate flowers: pedicels 1.3-1.6 mm long, becoming 2.9-3.3 mm in fruit; calyx-lobes 6, lanceolate to narrowly ovate, 1.4-2.3 mm long at anthesis, 2-3.5 mm long in fruit, acute, entire, ciliate, abaxially pubescent; styles united only at the base or up to 1/3 their length, stigmatic surfaces papillate. Fruit 3-4.5 mm long, 6-8 mm broad; columella 2-2.7 mm long; seeds nearly spherical, 3-4 mm long, brownish-black with a tawny mottling when mature.

DISTRIBUTION: southern Arizona and possibly New Mexico south into central and western Mexico (Map 1).

REPRESENTATIVE SPECIMENS: — ARIZONA: GRAHAM CO., Turkey Creek, 6 mi W of Point of Pines, 70 mi E of San Carlos, *Bohrer 439* (ARIZ). MARICOPA CO., Camp Creek, *Harrison & Hastings 6615* (ARIZ). PIMA CO., Sabino Canyon, Santa Catalina Mountains, *Kearney & Peebles 10320* (ARIZ); Baboquivari Canyon, *Kearney & Peebles 14982* (ARIZ). SANTA CRUZ CO., Patagonia Mountains, cliffs E of the old Flux Mine, ca. 5000 feet, *Niles, Mason & Williams 172* (ARIZ). YUMA CO., Castle Dome Mountains, *Arnold s.n.* (16/IX/1937) (ARIZ).

MEXICO. CHIHUAHUA: above Tinaja Canyon, W of Vieja Casas Grandes, *Tucker 2449* (ARIZ). HIDALGO: hills above El Salto, *Pringle 11303* (MICH). JALISCO: 18 mi S of Valparaiso, *McVaugh 17685* (MICH).

As pointed out by McVaugh (1961), the name *T. nepetifolia* has been 'loosely interpreted by recent botanists . . . to apply to a wide variety of herbaceous plants with the stems erect or nearly so . . . from Arizona and eastern United States to Guatemala.' The responsibility for this state of affairs rests mainly on Mueller (1866), who rather ineptly combined most of the taxa in the noseburn complex under the name *T. nepetifolia* while at the same time placing part of the specimens of *T. ramosa* under a different species name in another section of the genus. Johnston (1962) rectified the confusion with regard to *T. ramosa* but by combining all the noseburn taxa arrived at a concept of *T. nepetifolia* even more inclusive than that of Mueller.

Part of the difficulty in defining the limits of *T. nepetifolia* has been due to uncertainty with regard to its typification. Fortunately, through the courtesy of Dr. F. Bellot Rodriguez, director of the Instituto Cavanilles at Madrid,

we have obtained photographs of the two sheets which presumably served as the basis of Cavanilles' description. Johnston (1962) cited '*Sessé and/or Mociño*' as the collectors of the type, but as indicated by Mueller (1866), the specimens were actually collected by Née between Ixmiquilpan and Zimapan.

These specimens of Née, which are rather accurately (though somewhat crudely) depicted in Cavanilles' plate, have a leaf shape suggestive of *T. betonicifolia* or *T. urticifolia*, and rather closely match the Mexican specimens cited above. The Arizona population referred by us to *T. nepetifolia* agrees with the Mexican plants fairly well, although it differs in having generally more bluntly toothed leaves and a tendency to reddish male flowers. It is possible that these Arizona plants represent a distinct subspecies of *T. nepetifolia* or even a distinct species, but until the Mexican populations have been thoroughly studied there seems little utility in creating a special taxon for the small outlying race in Arizona.

As noted under *T. brevispica*, that species is rather similar to *T. nepetifolia* in some respects but differs in its twining habit and dimorphic fruits. The two species are allopatric in the United States, although further exploration may show their ranges to overlap in Chihuahua or northern Nuevo León. The bulk of the U. S. specimens which have passed as *T. nepetifolia* really belong to *T. ramosa*, which typically differs in its narrower more finely toothed leaves, greenish male flowers, and slender smooth styles. Both species are allopatric over much of the state of Arizona, and detailed studies of their habitat preference would probably be rewarding.

7. **Tragia ramosa** Torr. Ann. Lyc. N. Y. **2:** 245. 1828. (Figs. 5, 12, 23)

TYPE: 'sources of the Canadian' [evidently in SE Colorado], Long's Expedition, *James* (NY!).

Tragia angustifolia Nutt. Trans. Amer. Phil. Soc. (n.s.) **5:** 172. 1837.

Fig. 23. Habit, *Tragia ramosa (C. L. & G. York 55234)*.

TYPE: 'on the prairies of the Red River, in arid situations', *Nuttall* (K, lectotype!; NY, isotype!).[5]

Tragia scutelariifolia Scheele, Linnaea **25**: 587. 1852. TYPE: New Braunfels, Texas, July 1846, *Lindheimer 521* [Fascicle III] (B, not seen, perhaps destroyed).

Tragia ramosa var. ? *leptophylla* Torr. Bot. Mex. Bound. 201. 1859. LECTOTYPE: Texas, 'near Howard's Springs' [SW Crockett Co.], *Bigelow* (NY!). PARATYPE: 'New Mexico' [probably also from W Texas], *Wright 1796* (G, NY!).

Tragia stylaris Muell. Arg. Linnaea **34**: 180. 1865.

Tragia stylaris α *latifolia* Muell. Arg. loc. cit. Type: New Mexico, *Fendler 776* (G!).

Tragia stylaris β *angustifolia* Muell. Arg. loc. cit. TYPE: New Braunfels, Texas, July 1846, *Lindheimer 521* [Fascicle III] (G!).

Tragia stylaris γ *leptophylla* (Torr.) Muell. Arg. op. cit. 181.

Tragia nepetifolia ξ *ramosa* (Torr.) Muell. Arg. in DC. Prodr. **15 (2)**: 934. 1866.

Tragia nepetifolia β *latifolia* Muell. Arg. loc. cit. TYPE: 'Novo Mexico' [probably W. Texas], *Wright 1794* (G, GH, syntypes!).[6]

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5. Johnston (1962) suggested that the type of this taxon might be at BM. No sheets labelled as such were seen there, but specimens matching those at Kew and New York were mingled on one of the sheets of *T. betonicifolia*. In view of the labelling confusion of the BM specimens, choice of the Kew collection as lectotype seems desirable.

6. The two sheets of *Wright 1794* at the Gray Herbarium apparently represent several different collections made during 1851 and 1852, as no less than 4 different species are included: *T. amblyodonta*, *T. brevispica*, *T. nepetifolia* and *T. ramosa*. The specimens could have come from widely separated areas between eastern Sonora and the Pecos River, as indicated in the tabulation of localities by Wooton (1906). Unless Wright's original labels are discovered, which now seems unlikely, it may be impossible to clarify the origin of this melange of taxa. The presence of material of *T. amblyodonta* resembling that of *Wright 1793* suggests that perhaps part at least of *Wright 1794* came from the Pecos River Valley, but this is only a presumption, and cannot be true for the fragments representing *T. nepetifolia*, which does not enter Texas.

Mueller (1866) also cited Mexican specimens of Aschenborn, Hartweg, and Virlet d'Aoust with his description of var. *latifolia*. It is possible that one of the elements contained in *Wright 1794* may represent the same subspecific taxon as the Mexican collections, but until the Mexican variants of *T. nepetifolia* are straightened out, it seems best to regard all of these collections as syntypes.

Tragia nepetifolia θ angustifolia Muell. Arg. loc. cit. TYPE: Texas, *Berlandier 2542* (G!).
Tragia nepetifolia η scutellariifolia (Scheele) Muell. Arg. loc. cit.
Tragia ramosa α latifolia (Muell. Arg.) Pax & Hoffm. Pflanzenr. IV. 147. IX. [Heft 68]: 40. 1919.
Tragia nepetifolia var. *leptophylla* (Torr.) Shinners, Southw. Nat. 6: 101. 1961.

Stems solitary or few to many from the crown of the woody taproot, 1-2 mm in diameter near the base, 12-50 cm tall, green, purplish-green or yellowish-green, simple to many-branched, erect, decumbent, trailing, sometimes with a tendency to twine; upper internodes 3-30 mm long, lower internodes 7-40(60) mm long. Leaf blades linear-lanceolate to ovate or basal leaves sometimes reniform, 1-4 cm long, 0.4-2 cm broad, apically acute, basally truncate to cordate, margins serrate, thin, green, pubescent, ciliate; petioles 2-20 mm long; stipules lanceolate to ovate, entire, 1.2-4.5 mm long, 0.5-1.8 mm broad at the base, persistent, ciliate, rarely abaxially sparsely pubescent. Racemes with the lowermost 1(2) nodes pistillate, the remaining 2-20 nodes staminate; bracts of the pistillate flowers lanceolate, ca. 1.5-2 mm long, ciliate, acute, entire or three-lobed, sometimes abaxially sparsely pubescent; bracts of the staminate flowers lanceolate, subcucullate, ca. 1.2-1.8 mm long, pubescent, entire. Staminate flowers: pedicels slender, 0.7-2 mm long, lower persistent part ca. 0.4-1.5 mm long; calyx-lobes 3(42%), 4(49%)-5(7%) (6), oblanceolate to narrowly obovate-oblong, 1-2.2 mm long, abaxially pubescent, entire, reflexed or spreading at anthesis; stamens (2) 3(20%) 4(35%) 5(31%) 6(11%) (7-10), filaments thickened and fleshy, 0.3-1 mm long, connate basally. Pistillate flowers: pedicels 1-1.5 mm long, becoming 2-2.5 mm in fruit; calyx-lobes (5) 6(97%) (7), lanceolate to elliptic-lanceolate, 0.8-2.5 mm long at anthesis, 1.5-3 mm long in fruit, acute, entire, ciliate, abaxially pubescent; styles connate up to 1/3 their length; stigmatic surfaces not papillate (except slightly so in aberrant specimens). Fruit 3-4 mm long, 6-8 mm broad; columella 1.5-2.6 mm long; seeds nearly spherical, 2.5-3.5 mm long, brownish-black with a tawny mottling when mature.

DISTRIBUTION: open areas, often in disturbed habitats, Missouri and Arkansas west to California, Nebraska and Colorado south into Mexico (Map 6).

REPRESENTATIVE SPECIMENS: — ARIZONA: GILA CO., 10 mi S of Pine, *Peebles & Fulton 9460* (ARIZ). ARKANSAS: BENTON CO., Glade, *Demaree 6911* (UARK). CALIFORNIA: SAN BERNARDINO CO., New York Mountains, *Alexander & Kellogg 1326* (ARIZ). COLORADO: BOULDER CO., Steamboat Mountain, 2 mi NW of Lyons, *Weber 3906*

(TEX). KANSAS: MEADE CO., 11.5 mi E and 18 mi S of Meade, *Horr & McGreggor 3870* (LL, KANU). MISSOURI: STE. GENEVIEVE CO., 1 mi N of Bloomsdale, *Hubricht B1526* (ARIZ). NEBRASKA: FRANKLIN CO., Look-out Mountain, *Tolstead 411275* (TEX). NEVADA: CLARK CO., Wilson's Ranch, *Clokey 8013* (GA, NCSC, NY, SMU). NEW MEXICO: GRANT CO., Mangas Springs, 18 mi NW of Silver City, *Metcalfe 65* (ARIZ). OKLAHOMA: KIOWA CO., Entrance to Quartz Mountain State Park, *Miller & Miller 1341* (PUL). TEXAS: TRAVIS CO., Knob Hill, 12 mi W of Austin, *Miller & Miller 922* (PUL). UTAH: WASHINGTON CO., 5 mi E of Virgin, *Hitchcock 3019* (PH).

When the inflated concept of *T. nepetifolia* held by Mueller (1866) and Johnston (1962) is dissolved into its components, probably the majority of the *Tragia* collections west of the Mississippi River are referable to *T. ramosa*. Although Torrey originally described the species in 1828, he later (in the Botany of the Mexican Boundary Survey) confused it with *T. urticifolia*. Mueller (1866) partially resolved the confusion by pointing out that *T. urticifolia* differed in its more coarsely papillate styles but introduced several new misunderstandings which have obscured relationships among the noseburn taxa up to the present time: (1) he applied the epithet *ramosa*, when transferring it to varietal status under *T. nepetifolia*, not to Torrey's plant but rather to specimens of *T. brevispica*; (2) he included specimens of *T. ramosa* in 3 different varietal names under *T. nepetifolia*; and (3) he placed other specimens of *T. ramosa* in the 3 different varieties of his *T. stylaris* in a different section. He thus succeeded in divorcing the epithet *ramosa* from any of the plants to which it should properly be applied, and as a result the application of the name *T. ramosa* has remained highly confused. Pax and Hoffmann (1919) actually managed to improve on Mueller's malpractice by using Torrey's epithet *ramosa* twice: once for a species placed in sect. *Leucandra*, and again for a variety of *T. nepetifolia*. Judging from their citations of specimens, Pax and Hoffmann applied the name *T. nepetifolia ramosa* mainly to the typical subspecies or race of *T. nepetifolia*, and not to the population here associated with Torrey's name. Shinners (1958) on the other hand did

apply the name *T. nepetifolia ramosa* to the plants here accepted as *T. ramosa.*

Shinners has more recently (1961) proposed to call the common Texas noseburns *T. nepetifolia* var. *leptophylla.* This is correct on strictly nomenclatural grounds, but it would be rather unfortunate if the epithet *leptophylla* were generally taken up, as the collections of Bigelow and Wright represent very aberrant plants of rather dubious status. No similar specimens to the original collections of *leptophylla* have ever been found, and it is possible that the small scraps gathered by Bigelow and Wright might be hybrids or even unusual growth forms of some species other than *T. ramosa.*

Fortunately, we believe that the question as to the status of var. *leptophylla* is rather academic, since *T. ramosa* is certainly not conspecific with *T. nepetifolia.* In distinct contrast to that species, *T. ramosa* has long, thin, nearly smooth styles, greenish male flowers, a more densely hispid ovary, and typically narrower more sharply toothed leaves. Because of its broad spectrum of variability, *T. ramosa* does include forms which may be difficult to distinguish from any of the other taxa of noseburns, especially in the absence of good flowers and fruits. Furthermore, occasional interspecific crosses may occur which obscure the specific lines; a possible cross with *T. brevispica* has already been cited, and the discovery of crosses with *T. betonicifolia* and *T. amblyodonta* would not be surprising.

Johnston (1962) was correct in exposing as worthless the supposed difference in stamen number used by Mueller and by Pax and Hoffmann to segregate *T. stylaris* into a different section. Actually the number of stamens in non-terminal male flowers varies from 3-5, while in terminal flowers it may reach up to 10 (a figure larger than that recorded by any previous workers). Future quantitative studies on taxa of the noseburns should clearly specify the position of male flowers measured in order to insure an accurate estimate of the range of variation in stamen number.

Fig. 24. Habit, *Tragia amblyodonta* (*K. & L. Miller 1178*), A-E. Variation in leaf shape. A, *T. L. Steiger 421;* B, *B. L. Turner 1023;* C, *B. C. Tharp s.n.* (10/VII/41); D, *B. H. Warnock 46805;* E, *L. H. Shinners 19583.*

8. **Tragia amblyodonta** (Muell. Arg.) Pax & Hoffm. Pflanzenr. IV. 147. IX. [Heft 68]: 51. 1919. (Figs. 13, 24)

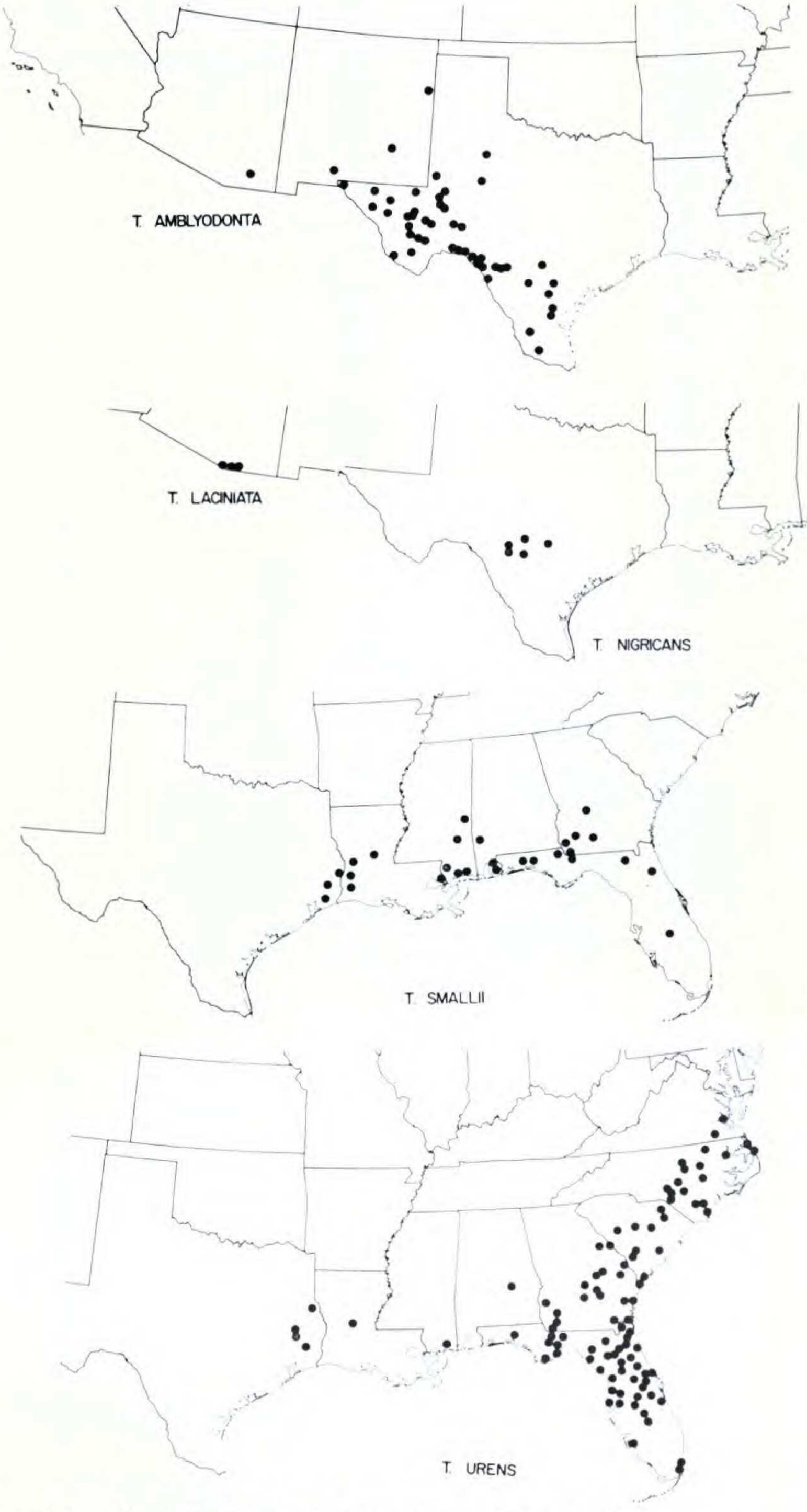
Tragia nepetifolia γ *amblyodonta* Muell. Arg. in DC. Prodr. **15 (2):** 934. 1866.

TYPE: Texas, 'alluvial soil, bottom of the San Pedro R. [Devil's River], July 6' [1852], *Wright 1793* (G, holotype!; data from isotype, GH!).

Stems few to many from the crown of the woody taproot, 1-1.6 mm in diameter near the base, 12-50 cm tall, green to grayish-green, few to many-branched, erect, decumbent or trailing; upper internodes 10-28 mm long, lower internodes 15-35 mm long. Leaf blades ovate, triangular or hastate, 1-4.5 cm long, 0.8-3 cm broad, apically acute to obtuse, basally truncate, cordate to hastate, margins crenate to serrate, thick, green, pubescent, ciliate; petioles 4-18(30) mm long; stipules ovate to rhombic-lanceolate, entire, 1-3.5(4.5) mm long, 0.6-1(1.6) mm broad at the base, persistent, ciliate, abaxially pubescent. Racemes with the lowermost 1 (2) nodes pistillate, the remaining 3-30 nodes staminate; bracts of the pistillate flowers lanceolate, ca. 0.9-1.3 mm long, ciliate, acute, entire or three-lobed, abaxially sparsely pubescent; bracts of the staminate flowers lanceolate, subcucullate, ca. 0.9-1.5 mm long, pubescent, entire. Staminate flowers: pedicels slender, 0.7-1 mm long, lower persistent part ca. 0.2-0.4 mm long; calyx-lobes 3(55%)-4(41%) (5), oblanceolate to obovate, 0.9-1.9 mm long, abaxially pubescent, entire, spreading to reflexed at anthesis; stamens (2) 3(67%)-4(28%) (5); filaments thickened and fleshy, 0.2-0.7 mm long, connate basally. Pistillate flowers: pedicels 0.3-0.4 mm long, becoming 1.5-2 mm in fruit; calyx-lobes (5) 6 (92%), lanceolate to narrowly elliptic, 1-2.3 mm long at anthesis, 2-3.5 mm long in fruit, acute, entire, ciliate, abaxially pubescent; styles connate only at the base or up to 1/3 their length, stigmatic surfaces papillate. Fruit 3-4.5 mm long, 5.5-8 mm broad; columella 1.8-2.5 mm long; seeds nearly spherical, 2.6-3.6 mm long, brownish-black with a tawny mottling when mature.

DISTRIBUTION: rocky areas, usually on limestone, southwest Texas to New Mexico, Arizona and Nevada (Map 7).

REPRESENTATIVE SPECIMENS: — ARIZONA: COCHISE CO., Tombstone, *Loomis & Peebles 5348* (ARIZ). NEW MEXICO: CATRON CO., Beaverhead, *Castetter 7104* (ARIZ). CHAVES CO., 20 mi S of Roswell, *Earle & Earle 291* (NY). DONA ANA CO., *Dunn 8463* (UNM). QUAY CO., San Juan, *Hershey 4010* (UNM). TEXAS: EL PASO CO., Scenic Drive above El Paso on Mt. Franklin, *Warnock 5752* (TEX). JIM HOGG CO., 7 mi N of Petroleum, *Tharp, Follansbee & Thompson 51-1533* (TEX). JIM WELLS CO., Alice-San Diego, *Tharp s.n.* (19/IV/1931) (TEX).



Map 7. Distribution of *Tragia amblyodonta.*
Map 8. Distribution of *Tragia laciniata* and *Tragia nigricans.*
Map 9. Distribution of *Tragia smallii.*
Map 10. Distribution of *Tragia urens.*

KLEBERG CO., 12.5 mi S of Kingsville a few miles W of Naval Air Station, *Johnston 541558* (TEX). LIVE OAK CO., Three Rivers, just N of town, *Thompson & Turner 24* (TEX). PECOS CO., 2 mi E of Ft. Stockton, *Warnock 46134* (TEX). TERRELL CO., 20 mi E of Dryden, *Parks, Turner & Warnock 72* (TEX). VAL VERDE CO., 1 mi N of the bridge over the Pecos River on Rt. 90, *Miller & Miller 1178* (PUL).

This plant was given specific status by Pax and Hoffmann under dubious auspices, since they did not see the type collection and misapplied the name to specimens of *T. glanduligera*. Shinners (1958), perhaps misled by this, suggested that var. *amblyodonta* might be the same as *T. teucriifolia* [*T. brevispica*]. In fact, *T. amblyodonta* has little in common with *T. brevispica*; it is occasionally viny but scarcely ever really twining. Typical specimens of *T. amblyodonta* are distinctive because of the greyish cast (due to denser pubescence) and broad shallowly few-toothed leaves. Sometimes one may encounter specimens with the dense pubescence of *T. amblyodonta* combined with the leaf shape of *T. ramosa*. We have no convincing evidence that such collections are interspecific hybrids, but it would not be surprising in view of the fact that *T. ramosa* appears to be the most closely related species.

As pointed out earlier, *T. amblyodonta* appears to differ from other U. S. species of *Tragia* in having a higher chromosome number: $2n = 110$ instead of 44. Correlated with this are larger stomata and pollen grains than are found in the other species. Additional cytological investigations on populations of *T. amblyodonta* would be desirable, in order to determine whether the apparent chromosomal difference is really a constant one.

9. **Tragia saxicola** Small, Fl. Southeast. U. S. 702. 1903. (Fig. 25)
TYPE: Florida, Dade County, rocky pine woods between the Everglades and Biscayne Bay, *A. H. Curtiss 2517* (NY!).

Stems few from the crown of the woody taproot, 0.7-1.2 mm in diameter near the base, 12-35 cm tall, green or yellowish-green, few to many-branched, erect; upper internodes 8-18 mm long, lower internodes 10-38 mm long. Leaf blades suborbicular, oblong to broadly ovate, 1.2-3 cm long, 1-2.2 cm broad, apically rounded to acute,

Fig. 25. Habit, *Tragia saxicola* (*A. H. Curtiss 2517*).

basally subcordate to cordate, margins crenate-dentate to serrate, thin, green, pubescent, ciliate; petioles 5-13 mm long; stipules lanceolate to narrowly ovate, entire, 1.5-4 mm long, 0.6-1.5 mm broad at the base, persistent, ciliate, abaxially pubescent. Racemes with the single lowermost node pistillate, the remaining 12-20 nodes staminate; bracts of the pistillate flowers lanceolate, ca. 0.8-1.4 mm long, ciliate, acute, entire or three-lobed, abaxially sparsely pubescent; bracts of the staminate flowers lanceolate, subcucullate, ca. 0.8-1.2 mm long, pubescent, entire. Staminate flowers: pedicels slender, 1.5-1.9 mm long, lower persistent part ca. 0.5-0.7 mm long; calyx-lobes 3(68%)-4(32%), obovate, 1.0-1.5 mm long, abaxially pubescent, entire, spreading to reflexed at anthesis; stamens 3(81%)-4(19%); filaments slender, thickened and fleshy, 0.4-0.6 mm long, connate basally. Pistillate flowers: pedicels 0.9-1.2 mm long, becoming 3.2-3.7 mm in fruit; calyx-lobes 6, lanceolate to ovate-lanceolate, 1.5-2.0 mm long at anthesis, 2.0-3.0 mm long in fruit, acute, entire, ciliate, abaxially pubescent; styles connate only at the base or up to 1/3 their length, stigmatic surfaces slightly papillate. Fruit 3.0-4.0 mm long, 6.0-7.0 mm broad; columella 1.7-2.1 mm long; seeds nearly spherical, 2.4-3.0 mm long, brownish-black with a tawny mottling when mature.

DISTRIBUTION: restricted to extreme southern Florida and the Keys typically in pine woods on limestone (Map 5).

REPRESENTATIVE SPECIMENS — FLORIDA: DADE CO., Lone Pine Key, *Atwater M-160* (GA); Biscayne Bay, *Curtiss 2517* (FLAS, GA, KANU, NY, PH, UARK). MONROE CO., Big Pine Key, *Eyles & Eyles 8192* (NCSC), *Killip 41089* (NO), *Killip 42441* (IA), *Small 3782, 3955* (NY).

This geographically isolated member of the noseburn complex is distinctive in habit because of its slender wiry stems and broad sharply toothed leaves, but in reproductive characters it is not very different from the Texas noseburns. Possibly *T. betonicifolia* is the closest species vegetatively, but the pistillate calyx of *T. saxicola* is more like that of *T. ramosa*. A relationship with *T. urticifolia* also seems evident, but that plant has narrower leaves and longer persistent staminate pedicels.

10. **Tragia laciniata** (Torr.) Mull. Arg. Linnaea **34:** 182. 1865; in DC. Prodr. **15(2):** 933. 1866. (Fig. 26)

Tragia urticifolia var. *laciniata* Torr. Bot. U. S. Mex. Bound. 200.

Fig. 26. Habit, *Tragia laciniata* (*R. H. Peebles et al. 5641*).

1858. LECTOTYPE: 'New Mexico', *Wright 1795* (NY!).

Stems few to many from the crown of the woody taproot, 1.3-1.5 mm in diameter near the base, 25-50 cm tall, green to purplish-green, few to many-branched, erect to decumbent; upper internodes 15-20 mm long, lower internodes 20-30 mm long. Leaf blades 3-divided, 2.5-4 cm long, the segments acute, their margins irregularly coarsely toothed, thin, green, pubescent, ciliate; petioles 7-18 mm long; stipules lanceolate, acute, entire, 1-2.8 mm long, 0.6-1.2 mm broad at the base, persistent, ciliate or abaxially sparsely pubescent. Racemes with single lowermost node pistillate, the remaining 10-20 nodes staminate; bracts of the pistillate flowers lanceolate, ca. 0.5-1.5 mm long, ciliate, acute, entire or 3-lobed; bracts of the staminate flowers lanceolate, subcucullate, ca. 0.5-1.5 mm long, pubescent, entire. Staminate flower: pedicels slender, 0.8-1.6 mm long, lower persistent part ca. 0.3-0.7 mm long; calyx-lobes 3(90%) (4), obovate to oblanceolate, 1-1.4 mm long, abaxially pubescent, entire, spreading to reflexed at anthesis; stamens 3; filaments slender, 3.5-4 mm long, connate basally. Pistillate flower: pedicels 0.6-1 mm long, becoming 2.5-3 mm in fruit; calyx lobes 6, lanceolate, 2-2.4 mm long at anthesis, 2.5-3 mm long in fruit, acute, entire, ciliate; styles connate 1/4-1/2 their length, stigmatic surfaces papillate. Fruit 3.5-4 mm long, 6-7 mm broad; columella 2-2.3 mm long; seeds nearly spherical, 3-3.2 mm long, brownish-black when mature.

DISTRIBUTION: Arizona and Sonora, Mexico, perhaps extending into New Mexico. All material examined was from Arizona, and the provenance of the Wright specimen is uncertain, as the label 'New Mexico' on his collections was used very loosely (Map 8).

REPRESENTATIVE SPECIMENS: — ARIZONA: *Clark 12540* (UNM). SANTA CRUZ CO., Sycamore Canyon, *Kearney & Peebles 14455* (ARIZ); Nogales to Ruby, *Kearney & Peebles 14916* (ARIZ, NY); between Nogales and Arivaca, *Peebles, Harrison & Kearney 5641* (ARIZ). (NEW MEXICO?): *Wright 1795* (PH).

Tragia laciniata is vegetatively the most distinctive of the U. S. species; the three-parted leaves are quite unmistakable. Pax and Hoffmann (1919) note its similarity to the South American *T. pinnata*, but the resemblance is probably due to parallelism. In reproductive characters *T. laciniata* agrees with members of the noseburn complex and is perhaps closest overall to some of the forms of *T. nepetifolia*.

11. **Tragia nigricans** Bush in Small, Fl. Southeast. U. S. 702. 1903; Missouri Bot. Gard. Report. **17:** 122. 1906. (Fig. 27)

TYPE: Texas, upper Hondo, common in woods, June 1885, *Reverchon 1594* (NY, syntype!).

Stems solitary or few from the crown of the woody taproot, 1-2 mm in diameter near the base, 15-55 cm tall, purplish-green to grayish-green, turning black in drying, simple or few-branched, erect; upper internodes 9-19 mm long, lower internodes 13-45 mm long. Leaf blades oblong to oblong-lanceolate, 3-7 cm long, 1-2.5 cm broad, apically and basally acute, margins deeply dentate, thick, green, pubescent,

Fig. 27. Habit, *Tragia nigricans* (*K. & L. Miller 1173*).

ciliate; petioles 1-5 mm long; stipules lanceolate, attenuate, entire, 2.5-6 mm long, 0.5-1 mm broad at the base, persistent, ciliate. Racemes with the single lowermost node pistillate, the remaining 2-5 nodes staminate; bracts of the pistillate flowers lanceolate, ca. 2-2.6 mm long, ciliate, acute, entire or three-lobed; bracts of the staminate flowers lanceolate, ca. 1-2 mm long, pubescent, entire. Staminate flowers: pedicels slender, 1.3-1.6 mm long, lower persistent part ca. 0.2-0.4 mm long; calyx-lobes 3(64%)-4(32%) (5), oblanceolate to narrowly ovate-oblong, 1.5-2.5 mm long, abaxially pubescent, entire, reflexed at anthesis; stamens (3) 4(48%)-5(49%) (6); filaments slender, 0.7-1.3 mm long, connate 1/3-1/2 or more their length. Pistillate flowers: pedicels 0.7-1 mm long, becoming 2-3 mm in fruit; calyx-lobes (5) 6(96%), narrowly rhombic-lanceolate, 1-2.3 mm long at anthesis, 2.4-4 mm long in fruit, acute, entire, ciliate; styles connate only at the base, stigmatic surfaces very slightly papillate. Fruit 3-3.5 mm long, 6.5-7 mm broad; columella 1.7-3.2 mm long; seeds nearly spherical, 2.5-3.2 mm long, brownish-black when mature.

DISTRIBUTION: restricted to a small area in south central Texas, in rocky soil of open woods and fields (Map 8).

REPRESENTATIVE SPECIMENS: — TEXAS: COMAL CO., Fischer's Store, *Palmer 12194* (TEX). KERR CO., limestone river bluffs near Kerrville, *Palmer 33811* (NY). MEDINA CO., Upper Hondo, *Reverchon 1594* (SMU). REAL CO., ca. 4 mi N of Leakey on Ranch Road 336, *Miller & Miller 1164* (PUL); Leakey, *Palmer 10162* (M). UVALDE CO., Garner State Park, *Miller & Miller 1173* (PUL), *Turner 3855* (TEX).

Tragia nigricans is one of the most distinctive species of the genus of those occurring in the U. S. The paucity of existing herbarium material may be misleading insofar as indicating the range and relative abundance of the species; additional localities on the Edwards Plateau may be expected. The general form of the leaves and the unique way in which the filaments in the staminate flowers are united one-half or more their length to form a cylinder set *T. nigricans* apart from the other U. S. species.

Section 2. LEPTOBOTRYS (Baill.) Muell. Arg. Linnaea **34**: 183. 1865; DC. Prodr. **15(2)**: 946. 1866.

Allosandra Raf. Aut. Bot. 51. 1840. LECTOTYPE: *Allosandra lanceo-*

lata Raf. (superfluous name for *Tragia innocua* Walt. = *T. urens* L.).

Leptobotrys Baill. Étud. Gén. Euphorb. 478. TYPE: *Leptobotrys discolor* Baill. (= *T. urens* L.).

Low perennial herbs, not twining; stem with stinging hairs but plants not severely stinging; leaves entire or rather coarsely and irregularly toothed or lobed; inflorescences opposite leaves or terminal on lateral leafy branches; staminate flower with 4 or 5 (rarely 6) calyx-lobes; stamens 2 (rarely 3); filaments thickened and fleshy, connate basally; pollen grains 'pseudocolpate', the operculum diffuse; pistillode flattened between the filaments, laminar; pistillate flower with 6 calyx-lobes; styles connate below, ventrally more or less papillate; seeds 3-4.5 mm long.

This section is here delimited so as to include only the two species of the Southeastern United States: *T. smallii* and *T. urens*.

Although Mueller (1866) and at first Pax (1890) accepted *Leptobotrys* as a section of *Tragia*, primarily on the basis of the androecium of only 2 stamens, Pax and Hoffmann (1919) submerged it as a synonym of their sect. *Eutragia*. The discovery of the characteristic pollen configuration in both *T. urens* and *T. smallii*, together with the androecial difference, would seem to justify reviving the section again. *Tragia urens*, with its peculiarly shaped leaves and tendency to monopodial stems, is furthermore very different from the other U. S. species in habit. However, *T. smallii* closes the gap to some extent, since it agrees better with the noseburn Tragias in leaf shape and inflorescence.

Although the taxa of sect. *Leptobotrys* do not appear to have any close ties with the North American representatives of sect. *Tragia*, it is not obvious which of the neotropical taxa of *Tragia* is closest. The similarity in pollen in sect. *Bia* is suggestive, but the male flowers of that group are very different by virtue of their many stamens and well-developed disk glands. Perhaps some of the South American species of sect. *Leucandra* (sensu Pax and Hoffmann, 1919) are most nearly related, but this is hardly more than a guess in our present state of knowledge.

12. **Tragia smallii** Shinners, Field & Lab. **24:** 37. 1956. (Figs. 15, 28)

TYPE: Louisiana, Vernon Parish, 1 mi S of Mayo. *McVaugh 8461* (SMU, holotype!; TEX, isotype!).

Tragia betonicifolia sensu Small, Fl. S. E. U. S. ed. 2, 702. 1913; and Pax & Hoffm. Pflanzen. IV. 147. IX. [Heft 68]: 62. 1919; non Nutt. (1837).

Stems solitary to few from the crown of the woody taproot, 1-2 mm in diameter near the base, 12-25 cm tall, purplish-green to grayish-green, simple to few-branched, erect; upper internodes 6-35 mm long, lower internodes 7-16 mm long. Leaf blades orbicular to elliptic, 2-4 cm long, 0.8-2.5 cm broad, apically rounded to acute, basally rounded to obtuse, margins coarsely serrate or crenate to lobed,

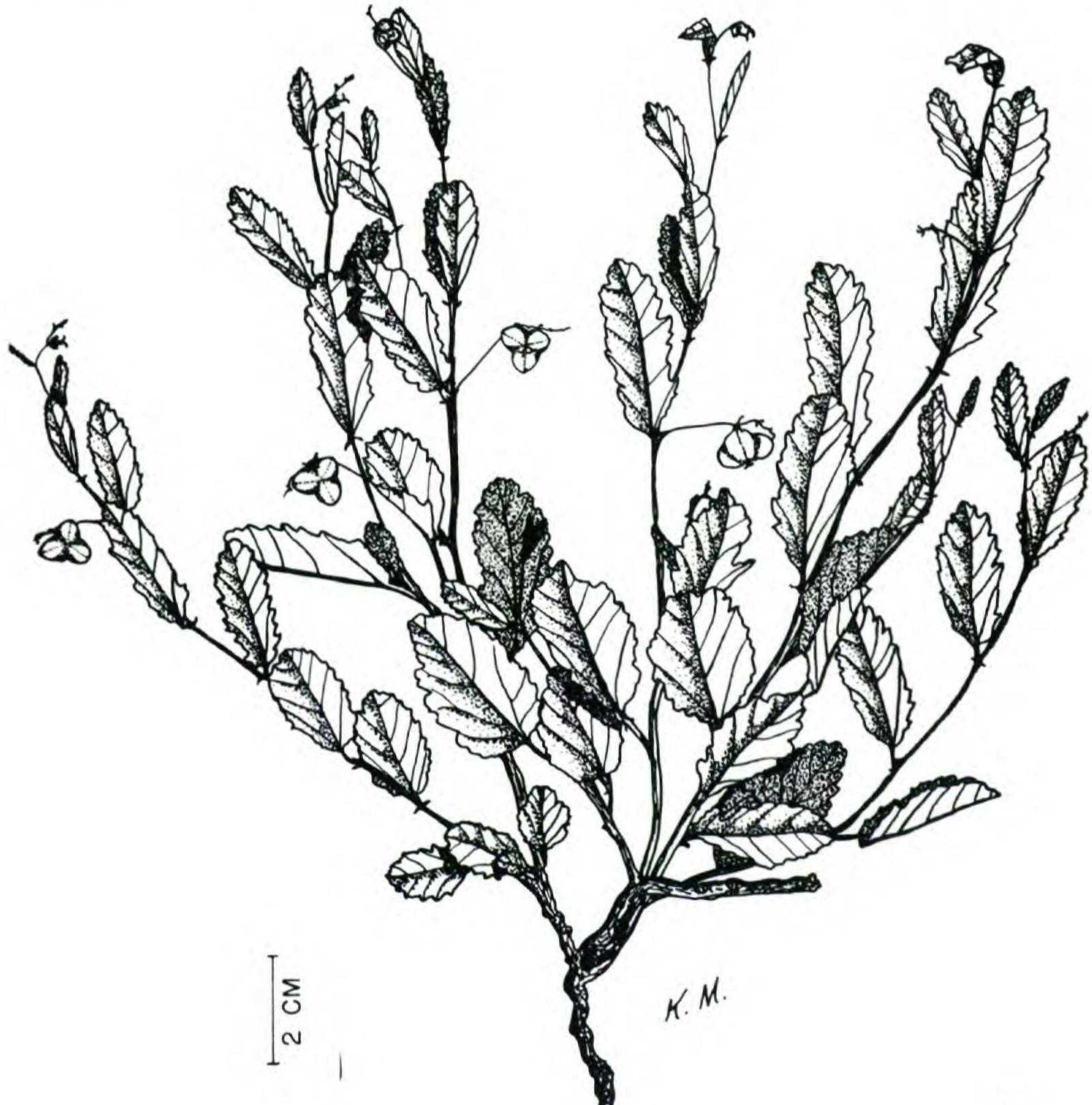


Fig. 28. Habit, *Tragia smallii* (*K. & L. Miller 865*).

thick, green, pubescent, ciliate; petioles 1-4 mm long; stipules lanceolate to narrowly ovate, entire, 1.5-3.8 mm long, 0.7-1.5 mm broad at the base, persistent, ciliate, pubescent. Racemes with the lowermost 1 (2) nodes pistillate, the remaining 4-11 nodes staminate; bracts of the pistillate flowers lanceolate, ca. 1.5-2.5 mm long, ciliate, acute, entire or three-lobed, sometimes abaxially sparsely pubescent; bracts of the staminate flowers lanceolate, subcucullate, ca. 0.8-1.2 mm long, pubescent, entire. Staminate flowers: pedicels slender, 1.5-1.9 mm long, lower persistent part ca. 0.4-0.6 mm long; calyx-lobes 4(50%)-5 (40%) (6), lanceolate to narrowly ovate, 0.9-1.5 mm long, abaxially pubescent, entire, spreading at anthesis; stamens 2(95%) (3); filaments thickened and fleshy, flattened laterally, 0.2-0.5 mm long, connate basally. Pistillate flowers: pedicels 0.5-1 mm long, becoming 2.8-3.4 mm in fruit; calyx-lobes 6, linear, 1.3-1.7 mm long at anthesis, 1.5-2.3 mm long in fruit, acute, entire, ciliate, abaxially pubescent; styles connate about 1/4 their length, stigmatic surfaces roughened but not papillate. Fruit 5-7 mm long, 9-13 mm broad; columella 2.2-3.2 mm long; seeds slightly elongated, 4-4.5 mm long, brownish-black with tawny mottling when mature.

DISTRIBUTION: Florida to east Texas along the gulf coast typically in dry sandy soil at the edge of woods and along roadsides (Map 9).

REPRESENTATIVE SPECIMENS: — ALABAMA: BALDWIN CO., 3 mi N of Foley, *Whitehouse 24262* (SMU). FLORIDA: HIGHLANDS CO., Sebring, *Garrett s.n.* (10/V/1948) (FLAS). GEORGIA: DECATUR CO., 1.3 mi SSW of Faceville, *Thorne & Davidson 17122* (IA). LOUISIANA: Vernon Parish, 2 mi W of Leander, *Webster & Wilbur 3249* (SMU). MISSISSIPPI: LAUDERDALE CO., 18 mi SW of Quitman on Route 18, *Miller & Miller 865* (PUL). TEXAS: HARDIN CO., 7 mi S of Kountze, *Whitehouse 23253* (SMU). NEWTON CO., 3 mi N of the junction of Route 63 and Farm Road 692, *Thompson & Turner 151* (TEX).

Shinners was correct in giving a new name to the plant which Small (1913) and Pax and Hoffmann (1919) had confounded with *T. betonicifolia* of Nuttall; the latter occurs only to the west of the range of *T. smallii*. Vegetatively, *T. smallii* resembles *T. saxicola* to some extent, but its pollen grains agree closely with those of *T. urens*. Since it furthermore has staminate flowers with only 2 stamens and a flattened pistillode, it would appear to belong closest to *T. urens*.

13. **Tragia urens** L. Spec. Pl. ed. 2: 1391. 1763. (Figs. 16, 29)
Ricinus parvus urens, foliis quercinis, virginianus Plukenet, Alm. bot. 320, t. 107. f. 5. 1696. (No type present in Herb. Sloane, BM).
Tragia innocua Walt. Fl. Carol. 229. 1788. (No type present in Herb. Walter, BM).
Tragia urens α subovalis Michx. Fl. Bor. Amer. **2:** 175. 1803. TYPE: Herb. Michaux (P!).[7]
Tragia linearifolia Ell. Sketch. **2:** 563. 1824. TYPE: southern Georgia (not seen).
Tragia urens β lanceolata Michx. loc. cit. (based on *T. innocua* Walt.).
Tragia urens δ linearis Michx. loc. cit. TYPE: Herb. Michaux (P!).
Allosandra lanceolata Raf. Aut. Bot. 51. 1840.
Allosandra verbenifolia Raf. loc. cit.
Leptobotrys discolor Baill. Étud. gén Euphorb. 479, t. 2, f. 17, 18. 1858. SYNTYPES: *Michaux, Leconte, Noisette* (P!).
Tragia discolor (Baill.) Muell. Arg. in DC. Prodr. **15 (2):** 946. 1866.
Tragia discolor α subovalis (Michx.) Muell. Arg. loc. cit.
Tragia discolor β cuneata [f.] a, *latifolia* Muell. Arg. loc. cit. TYPE: Carolina, *Bosc* (not seen).
Tragia discolor β cuneata [f.] b, *lanceolata* (Michx.) Muell. Arg. loc. cit.
Tragia discolor δ linearis (Michx.) Muell. Arg. in DC. Prodr. **15 (2):** 947. 1866.
Tragia urens var. *α innocua* (Walt.) Pax and K. Hoffm. Pflanzenr. IV 147. IX [Heft 68]: 58. 1919.

Stems solitary or few from the crown of the woody taproot, 1-2.2 mm in diameter near the base, 20-50 cm tall, purplish-green to grayish-green, few to many-branched, erect; upper internodes 7-15 mm long, lower internodes 10-25 mm long. Leaf blades broadly oblanceolate to linear, 2-8 cm long, 2-14 mm broad, apically acute to rounded, basally acute to attenuate, margins entire, round-toothed to lobed, thick, green, pubescent, ciliate; petioles 0-2 mm long; stipules linear to lanceolate, entire, 1.5-6 mm long, 0.3-1.1 mm broad at the base, persistent, ciliate, pubescent on both surfaces. Racemes with the lowermost 1 (2) nodes pistillate, the remaining 3-45 nodes staminate; bracts of the pistillate flowers lanceolate, ca. 1-2.5 mm long, ciliate, acute, entire or three-lobed, abaxially sparsely pubescent; bracts of the staminate flowers lanceolate, subcucullate, ca. 1-1.5 mm long, pubescent, entire. Staminate flowers: pedicels slender, 1.3-2 mm long, lower persistent part ca. 0.3-0.6 mm long; calyx-lobes 4(73%)-5(27%), broadly lanceolate to ovate, 1-1.5 mm long,

7. There are 3 specimens on 2 sheets of *T. urens* in the Michaux Herbarium at Paris; these presumably represent the types of the varieties described in Michaux's book, but the individual specimens are not labelled with the varietal epithets.

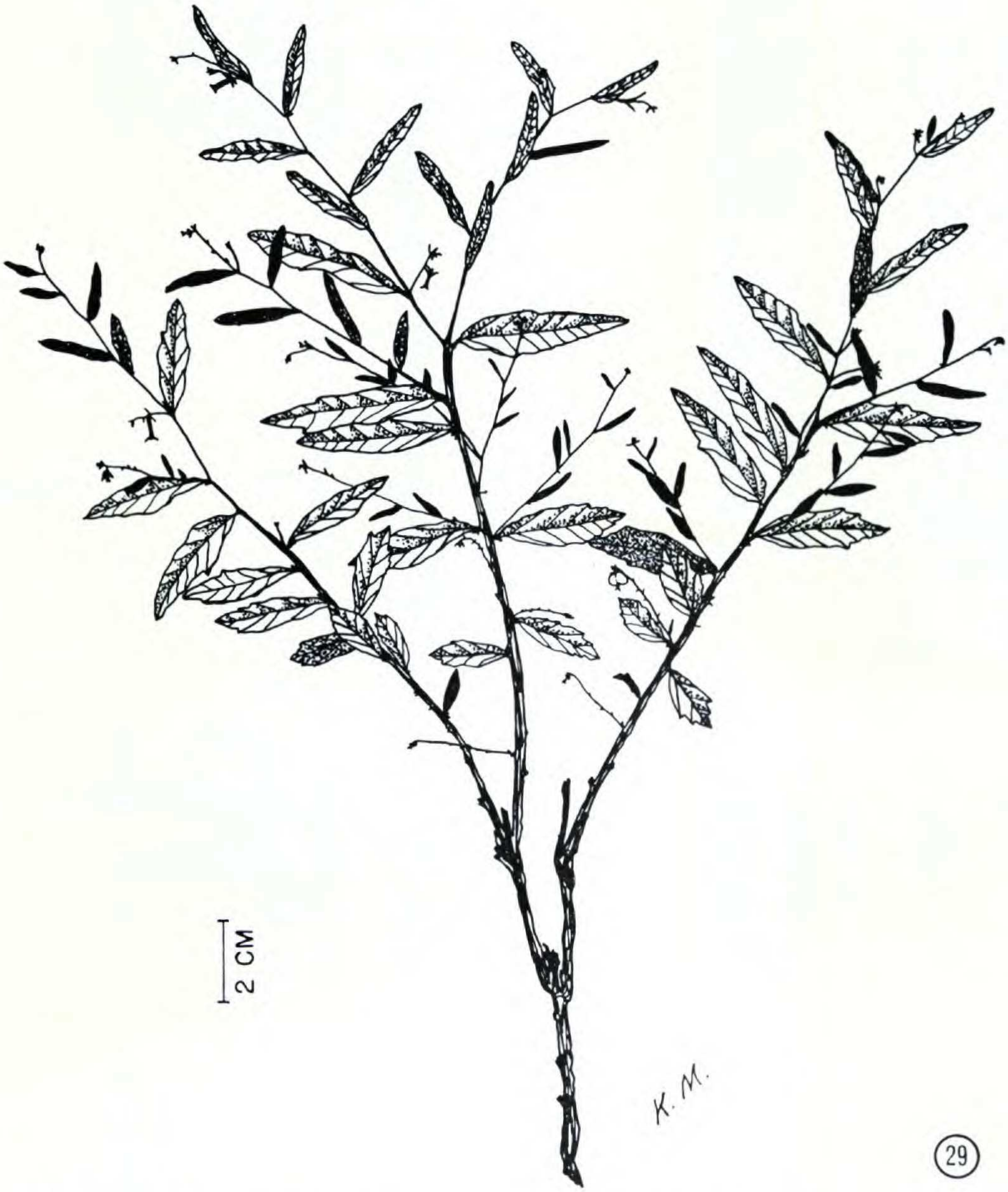


Fig. 29. Habit, *Tragia urens* (*K. & L. Miller 776*).

abaxially pubescent, entire, spreading at anthesis; stamens 2(91%) (3); filaments thickened and fleshy, 0.2-0.4 mm long, connate basally. Pistillate flowers: pedicels 0.6-1 mm long, becoming 3.5-4 mm in fruit; calyx-lobes 6, linear, 1-1.5 mm long at anthesis, 1.5-1.8 mm long in fruit, acute, entire, ciliate, abaxially pubescent; styles connate 1/4-1/3 their length, stigmatic surfaces roughened but not papillate. Fruit 3-4 mm long, 7-8 mm broad; columella 1.9-2.6 mm long; seeds slightly elongated, 3-4 mm long, brownish with a tawny mottling when mature.

DISTRIBUTION: Virginia south to Florida and west to east Texas, in dry sandy soil or woods and clearings (Map 10).

REPRESENTATIVE SPECIMENS: — ALABAMA: MONTGOMERY CO., Montgomery, *Sargent s.n.* (16/V/1955) (SMU). FLORIDA: DADE CO., South Miami, *Moldenke 5857* (NY). GEORGIA: RANDOLPH CO., 1 mi W of Coleman, *Thorne & Muenscher 8154* (IA). LOUISIANA: RAPIDES PARISH, Alexandria, *Hale s.n.* (NY). MISSISSIPPI: JACKSON CO., Ocean Springs, *Tracy 4728* (NY). NORTH CAROLINA: PENDER CO., ca. 15 mi NW of Wilmington on U. S. 421, *Miller & Miller 776* (PUL). SOUTH CAROLINA: ALLENADE CO., 3.5 mi E of Sycamore, *Radford 5347* (NCSC). TEXAS: HARDIN CO., 4 mi W of Silsbee, *Thompson & Turner 103* (TEX). VIRGINIA: SOUTHAMPTON CO., 2 mi SW of Sebrell, *Smith & Hodgdon 1069* (ARIZ, FLAS, GA, IA, ISC, KY, NCSC, NO, NY, PH, SMU, TEX, UARK).

Linnaeus based *T. urens* on the treatment by Plukenet, citing Virginia as the type locality. Since there is no specimen of Plukenet in the Sloane Herbarium (BM), the species must be typified by the illustration and description. The picture, although rather crude, is sufficiently characteristic — when taken in conjunction with the locality —to fix the application of the name. The specific epithet is not very appropriate, since *T. urens* is the least painfully stinging of the U. S. species (hence Walter's substitute name); it seems possible that Plukenet may have somehow confounded reports of the stinging qualities of *T. urticifolia* in providing his original description.

As delimited here, the varieties proposed by Michaux and the *T. linearifolia* of Elliott do not seem worthy of maintaining at any taxonomic level. Long linear entire leaves occur sporadically throughout the range of the species and certainly do not appear to show any correlations with geographic distribution or with reproductive differences. The names of Rafinesque are as usual difficult to dispose of. The epithet and description of *Allosandra verbenifolia* Raf. are somewhat suggestive of *T. smallii*, and it is possible that it could prove to be the earliest name for that plant. However, we have not been able to locate any

specimens of *T. smallii* collected by Baldwin or Ware, as mentioned by Rafinesque; the only Baldwin collection examined (NY) proves to be *T. urens*. Until a type specimen is discovered, it seems quite unwarranted to take up a name as vaguely characterized as *Allosandra verbenifolia*.

In many ways *T. urens* is the most isolated of the U. S. species. Although its pseudocolpate pollen is shared by *T. smallii*, together with the low stamen number, it is vegetatively unlike that species in producing some of its inflorescences at the tip of leafy branches which give a 'pinnate' effect to the main stems. The inflorescence pattern approaches that of neotropical species such as *T. mexicana* more closely than does that of the other U. S. taxa. Furthermore, two collections were examined in which the plants were entirely pistillate; the inflorescences have 6-10 or more female flowers instead of only 1 or 2. Inflorescences with several pistillate flowers also occur in sects. *Zuckertia* and *Bia*, and it is thus of some interest that the inaperturate pollen grains in the latter group show a similarity to those of *T. urens*. It would appear that *T. urens* is a phytogeographically isolated taxon in the United States, with a completely different origin from the noseburn complex in Texas and adjacent states.

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APPENDIX

A TABULATION OF THE LINDHEIMER COLLECTIONS OF *Tragia* (based on examination of herbarium sheets and correlations by Blankinship (1907).

Fascicle	Fascicle no.	Collector's no.	Date	Identity & herbaria
I	176		1843	*T. betonicifolia* (MO)
II	307		1844	*T. brevispica* (GH, NY, P, SMU)

III	521	298	1846	*T. ramosa* (G, GH, MO, PH, SMU)
III	522	299	1846	*T. brevispica* (GH, MO, TEX)
				T. urticifolia (PH)
IV [?]	'307'		1847-48	*T. brevispica* (G, M, MO, NY, P)
IV	'521'		1847-48	*T. ramosa* (GH)
V	1154	139	1849 (Aug)	*T. brevispica* (GH, MO, PH, SMU)
V	1155	138	1849 (Jl)	*T. brevispica* (GH, MO, PH, TEX)
V	1156	74	1849 (Jl)	*T. brevispica* (GH)
V	1156	74	1849 (Jl)	*T. ramosa* (GH, MO, SMU, TEX)
V	1156	128	'1847'	*T. urticifolia* (MO)

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